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A FIVE-YEAR FIELD STUDY OF CODLING MOTH LARVAL HABITS AND ADULT EMERGENCE

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In the course of codling moth life-history studies the larvae were reared for several years in both orchard and insectary, but always in apples removed from the trees. It was therefore felt that information was desirable on the behaviour of larvae feeding naturally in growing fruit in the orchard, in particular on such phases as the relationship between the numbers of "wormy" fruits and larvae reaching maturity; the relative proportions of transforming and overwintering larvae; the date after which all larvae enter diapause; the effect of the date of larval maturity on the date of moth emergence the following spring; and the effect of apple variety on larval diapause. At the same time information was sought on the efficacy of tree bands, their possible use in population studies, and their value as a practical control measure under local conditions.

The studies were carried out in a small orchard at Vineland Station, Ontario, in which tree bands were used to trap the larvae, and the subsequent development of the larvae was followed in a nearby insectary.

DESCRIPTION AND HISTORY OF ORCHARD

The orchard consisted of a block 61 by 185 yards, running north-south, and comprising about 2.3 acres. It contained about 150 trees, mostly Ontario and McIntosh varieties but including Jonathan, Wealthy and Cranberry, about two-thirds of which were in full bearing and the remainder just beginning to bear. The trees were planted on a triangular system about 25 feet apart at the shortest distance (on different rows) so that the outer branches of the older trees touched in places. The orchard floor was very free from trash and although a buckwheat cover crop was sown in late spring there was little growth under the experimental trees where the ground was well tramped in the course of examination of bands and continuous gathering of dropped fruit. A spruce windbreak ran along the east side; a small woodlot was about 150 feet distant at the southern end, and the west and north were more or less open.

For several years before 1940 the entire orchard had been used for codling moth control plots and, since some spray materials failed to give control, the population increased. From 1940 to 1945, inclusive, the south half of the orchard received sprays of fungicides only; in 1940 five McIntosh and three Ontario trees gave a count of 21,679 fruits of which 20,269 or 93.5 per cent had deep codling moth injury, so that in 1941, when banding experiments were started in the unsprayed half a high codling moth population was present.

METHODS OF BANDING AND RECORDING

Five trees each of McIntosh and Ontario were chosen each year with regard first to the size of the crop and second to the freedom of the tree framework from cavities and crevices. All loose bark was carefully scraped off trunk and limbs from where smooth bark prevailed on the smaller branches to below ground level, the soil being finally compacted against the trunk. Three-ply burlap bands were placed around the trunks, with the ends overlapping a few inches, at six to ten inches above the ground level. The scraping was done early in the season as opportunity occurred and the bands applied the last week in June in time to catch the first maturing larvae. The bands were examined every other day and the number of larvae noted for each tree. All the large (normal) larvae, at each collection, were put in pint glass sealers with rolls of corrugated paper, those from the five McIntosh trees being kept separate from those taken on Ontario. Larvae parasitized by *Ascogaster quadridentatus* Wesm., distinguished by their small size, were counted and kept separate from normal larvae. The jars of normal larvae were at once transferred to a nearby insectary where moth emergence was recorded daily. All moths and adults of *Ascogaster* were released in the orchard after they emerged in the insectary. The insectary, situated about 150 feet east of the orchard, had wire screen on all sides and ceiling and a ridge roof open at both ends. The jars were arranged on shelves so that the sun could not shine directly on them.

Dropped apples were gathered frequently and after examination were piled in a broken circle about three feet from the trunk. This was done in the hope that larvae, still in the fruit when it fell, would be trapped in the band on the tree from which the fruit had fallen. An apple was considered wormy if it showed an exit hole or sufficient fresh frass to indicate that a larva was definitely established within.

CONSIDERATION OF BURLAP BANDS

Before detailing the results obtained from banding it might be well to take up a few points concerning the behaviour of mature larvae in the particular orchard where the studies were carried out, and the reliability of burlap bands as a basis for population and similar studies.

Movements and Disposition of Mature Larvae in Bearing Trees

In 1935, when the orchard was in process of reduction to its present size, five Greening trees with trunks about one foot in diameter were dismembered in March and closely scrutinized in the laboratory for codling moth cocoons. Of the 495 cocoons found 46 per cent were in the top, 13 per cent in the region of the main crotch and 41 per cent on the main trunk. This represented the final disposition of the larvae but for present purposes it is necessary to know by what route they arrived there and what proportion of the high percentage in the top passed over the main trunk before settling. To shed some light on this a single McIntosh tree, carrying a full crop, was carefully scraped and banded in 1941. Besides the band on the main trunk 32 additional bands were distributed over the framework of the tree and all were examined at two-day intervals. Of the approximately 2000 larvae taken in these bands 45 per cent were in the top of the tree,

17 per cent on the main limbs and 38 per cent on the trunk—a reasonable approximation to the Greening figures above. Now by what route did these larvae reach the bands in which they were found? The answer is that probably most of them wandered over much of the tree in searching for cocooning quarters; that some, taken in the trunk band, crawled down from the top of the tree and others, taken near the top, came out of "drops" on the ground via the trunk. In support of this are the following data: (1) Practically from the beginning of larval maturity, there were always larvae in the trunk band as well as in other bands. Early in the season, when there are few drops, experience has shown that more larvae come down the tree than go up (disregarding return trips which are common) so that at this time of year at least, a number of larvae taken in the trunk band must have come from fruit on the tree and in descending must have passed over other bands. (2) At the end of the season, when no fruit was left on the tree, larvae were taken in the most distal bands and, since they must have come from the ground, had passed other bands on the way. (3) Five of the bands had other bands both above and below and should therefore have taken no larvae had the latter entered the first band they reached; nevertheless the catches in these five bands were no lower than in others not so situated.

A direct observation bearing on the above was made in 1944 in the same orchard. On a lower main limb of a McIntosh, in bearing but young enough to have smooth bark to the ground, a mature larva was spotted. It went nearly to an outer tip and then, after various searchings, went down the trunk to within six inches of the ground. It then returned and going up another main limb examined two laterals almost to their tips and again descended the trunk to near the ground. Once more it ascended to the same main limb and examined two more laterals to the tips and finally

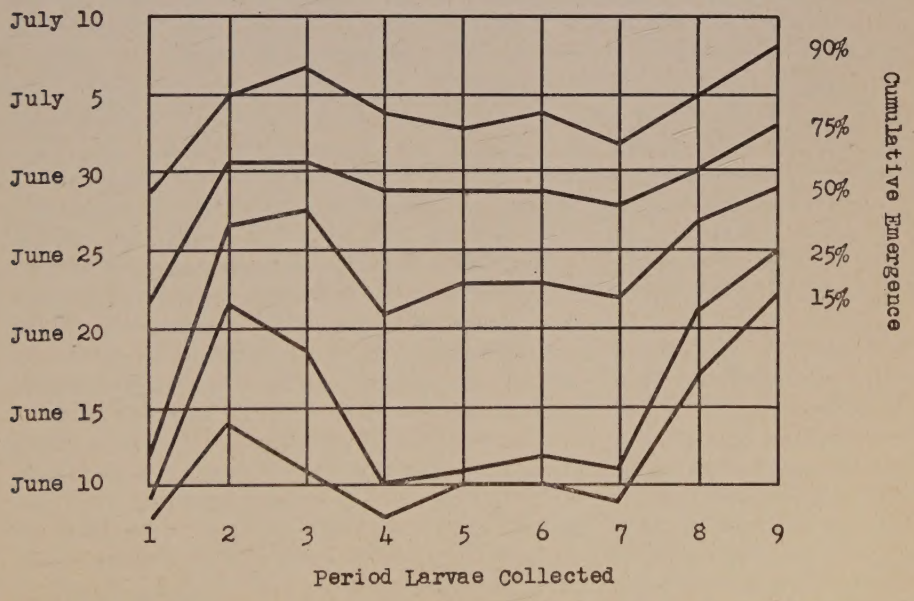

FIGURE 1. Emergence of codling moths in 1942 from larvae collected in 1941.

descended the main trunk to the ground. The time taken was about two hours. On two other occasions similar observations were made and it was found that by the observer assuming a certain position, the incident light rendered the larval threads clearly visible, and the whole trunk and main limbs were seen to be covered by a maze of these threads. There was no indication that the larvae followed one another, as the threads, apparently haphazard, covered every part of the trunk. It should be noted that by far the greater part of larval migration occurs at night.

Bands May Collect Larvae Other Than from the Tree Banded

Owing to the closeness of the trees and smoothness of the ground in the orchard it was expected that some larvae would wander for a distance and might be taken in a band on a tree other than that from which they came. It was felt, however, that this movement would be reciprocal and should not materially affect the numerical results though it might result in possible mixing of the larvae from McIntosh and Ontario varieties since these were in adjoining rows. In 1941 an Ontario tree, which bore not a single apple, nevertheless yielded 252 larvae from a trunk band. The tree happened to be surrounded by trees with good crops of wormy fruit but even so the large number of larvae taken was somewhat of a surprise especially since some small parasitized larvae were included in the catch.

Probable Proportion of Total Larvae Trapped

With regard to the multiple-banded tree how many larvae would the trunk band have caught in the absence of all the other bands? Unfortunately this cannot be answered directly but the relation of numbers of larvae to total fruits was 50 per cent on this tree, while in the same season on five other scraped McIntosh trees with a single trunk band this relationship varied from 38 to 68 per cent with an average of 50 per cent for the five trees. This may mean that one trunk band on a well-scraped tree would be as effective as many bands placed all over the tree.

The foregoing evidence appears to show that, in the case of a well-scraped tree, the great majority of larvae produced by that tree will pass over or enter the burlap trunk band. The question now arises as to how many of these larvae will be trapped in the band. Apart from what happened on the multiple-banded tree, the writer has observed, on several occasions, larvae crawling over the top of burlap bands without making any attempt to enter them. In 1942 a very limited trial was undertaken with two modifications of the burlap band. The three-ply burlap in both cases had a strip of black light-proof paper placed in the inner fold. In order to hold the burlap away from the trunk at its edges, so larvae would not just crawl over the outside of the band, a strip of wire screen about an inch and a half wide was crimped by running through the cogs between two meshed gear wheels. Two of these strips were first placed around the trunk so that the edges of the band rested on them and were thus held sufficiently away from the trunk to allow larvae to pass readily under. In the second modification, instead of the wire screen, two "necklaces" of small pieces of wood, about $1\frac{1}{2}$ by $\frac{1}{4}$ by 3/16 inches, were knotted with string to encircle the trunk at intervals of about $\frac{1}{4}$ inch with the long axis vertical. The wood happened to be rather soft and many larvae bored

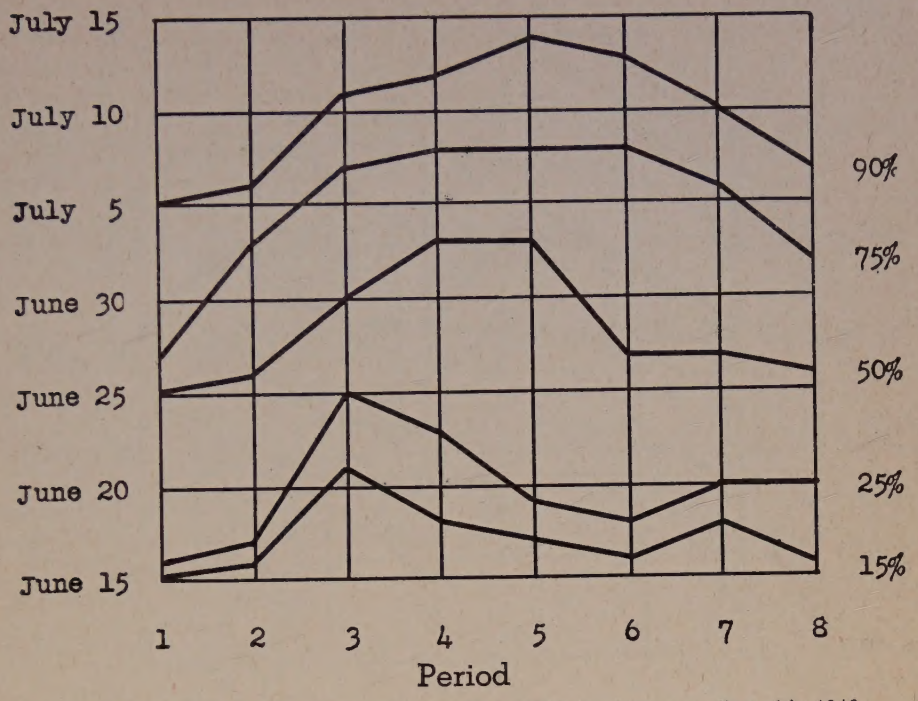

FIGURE 2. Emergence of codling moths in 1943 from larvae collected in 1942.

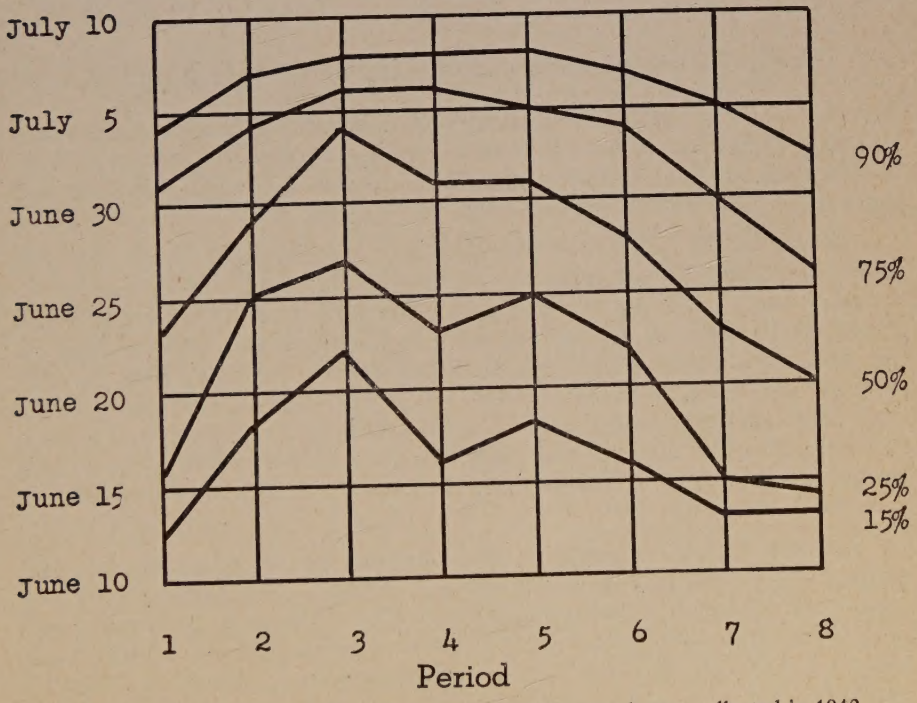

FIGURE 3. Emergence of codling moths in 1944 from larvae collected in 1942.

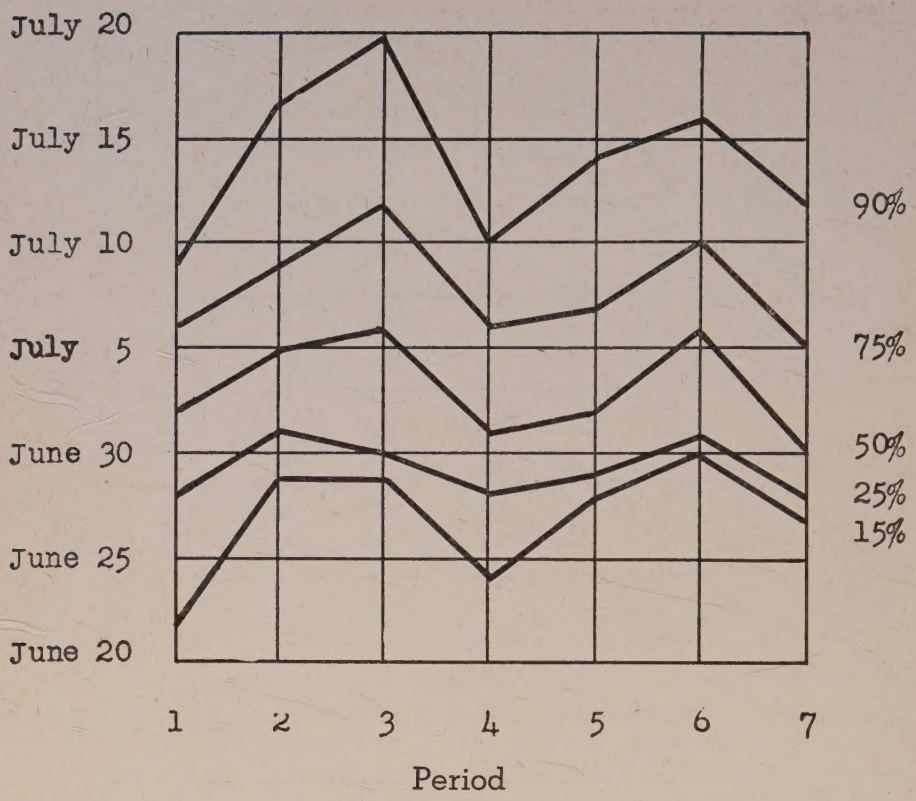

FIGURE 4. Emergence of codling moths in 1945 from larvae collected in 1944.

into the pieces. Only one of each of these modified bands was checked against the ordinary band. Two trees were used to test each type, and the modified and ordinary bands were changed over each week, nine changes being made after they were first placed on July 21 and 22.

In the case of the wire screen modification, of the 974 larvae taken in it and the check, 60 per cent were in the modified and 40 per cent in the ordinary band. The wood necklace modification was even more efficient for, of the 1331 larvae, 67 per cent were in the modified and 33 per cent in the ordinary band. These results must be considered indicative only since an insufficient number of trees was used. Also it should be noted that the bands were examined at weekly intervals whereas in the work detailed below the interval was only two days. It is probable that more larvae are taken when the interval is shorter because overcrowding is avoided.

To sum up the foregoing it would appear that if a tree is very well scraped the larvae will do a considerable amount of travelling over the framework in search of cocooning places so that a burlap trunk band should eventually catch all of them except those that succeed in finding a suitable spot in the top of the tree such as the depressions formed in partially-healed pruning scars. It is estimated (from the examination of the Green-

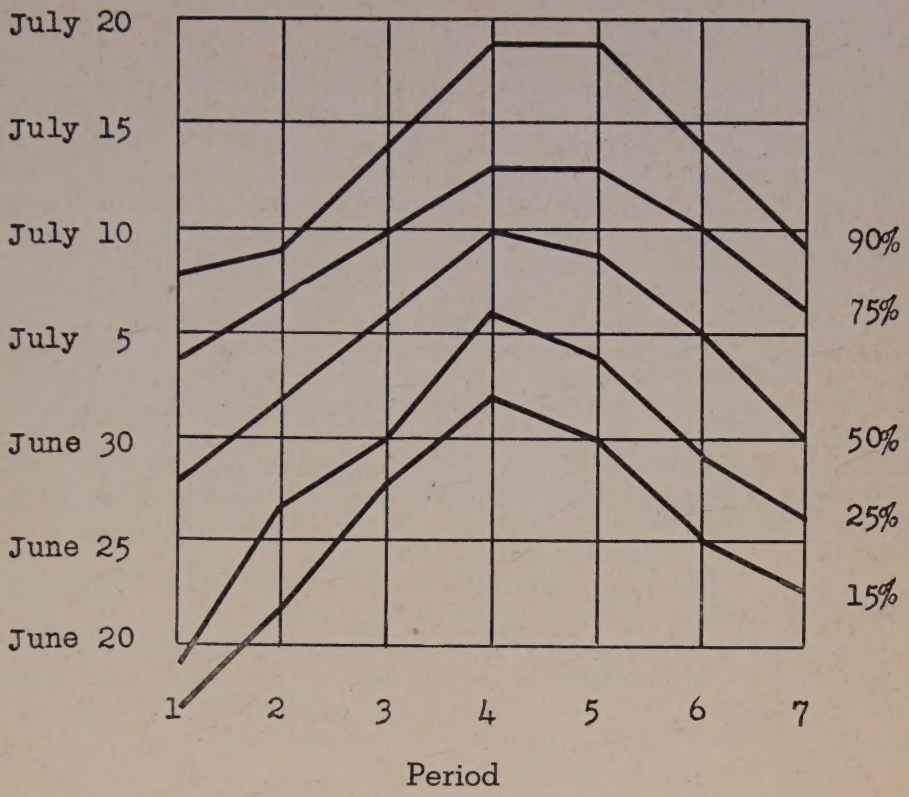

FIGURE 5. Emergence of codling moths in 1946 from larvae collected in 1945.

ing trees mentioned above) that such larvae avoiding the band may amount to 30 per cent of the total produced by the tree, exclusive of those destroyed by predators before cocooning. The larvae crawling off the tree permanently would tend to be replaced by a similar number leaving other trees. This would also apply to larvae leaving the tree in dropped fruit.

Effect of Condition of Orchard Floor

Since larvae will readily spin up in trash, such as bits of wood, twigs, hollow weed-stems, etc., the amount of such trash is likely to affect the number of larvae trapped in bands. H. R. Boyce dug out as many as 160 larvae from a small wooden container for poisoned mouse bait which had been left rotting on an orchard floor.

Effect of Predators

In the present study the effect of predators was not investigated, but a certain unknown proportion of the larvae produced by the trees was undoubtedly destroyed by them. Jaynes and Marucci (1947) have shown that under their conditions from 14 to 30 per cent of free larvae released in the orchards were attacked by predators, chiefly ants, within 24 hours. It is believed that predation was lower than this at Vineland Station.

Comments on Commercial Value of Bands

It will be seen from the above that, providing the orchard floor is free from trash and the trees well scraped and free from cavities, a minimum of about 70 per cent of the surviving larvae should be trapped in trunk bands. To obtain such results very thorough scraping is necessary, a time-consuming job and moreover one that must be done with care to avoid injury. To avoid the frequent removal of larvae, necessary until transformation ceases for the season, chemical bands have been used. Our experience with beta naphthol-oil treated bands was that they exert a marked deterrent effect until much of the chemical has weathered off. For example, in an experiment designed to find out whether chemical bands would remain toxic to larvae throughout the season it was found that of the 1651 larvae trapped in 90 banded trees 32 larvae per tree were taken in those bands remaining on the trees all season whereas only 10 larvae per tree were captured where bands were replaced with fresh ones five times during the season. Under local conditions the cost of effective scraping and banding is considered prohibitive and the use of DDT will probably render such measures unnecessary.

RESULTS FROM FIVE YEARS OF BANDING

Relationship Between Size of Crop and Larval Population

Over the five year period 1941 to 1945 the ten trees yielded a crop of 130,122 apples, and a total of 29,536 codling moth larvae were taken from the bands. Thus there was an average of about 590 larvae per tree per year. The figures for each year are given in Table 1.

TABLE 1.—PROPORTION OF TRAPPED CODLING MOTH LARVAE TO TOTAL FRUITS

Year	No. fruits	Larvae	% Larvae to fruits
1941	23,848	10,954	45.9
1942	15,358	2,666	17.4
1943	41,337	7,265	17.6
1944	22,218	3,657	16.5
1945	27,361	4,994	18.3

It will be noted that about a third of the total catch was taken in one year, 1941. That this year was particularly favourable for codling moth is shown by the percentage of larvae to fruits (*i.e.*, number of larvae per 100 fruits) which was two and a half times higher than in any of the other four years. The reason that 1941 was more favourable than the following four years is probably to be found in the higher prevailing temperatures during the important months of May, June and July. In Table 2 the differences from the 26-year normals for average monthly temperatures are given for the five years.

TABLE 2.—MONTHLY TEMPERATURE DIFFERENCES FROM 26-YEAR NORMALS DEGREES F.

Month	1941	1942	1943	1944	1945
May	3.4	1.8	−0.8	3.0	−4.9
June	3.0	−0.5	3.0	0.8	−2.4
July	1.4	−1.2	−1.2	0.1	−0.5

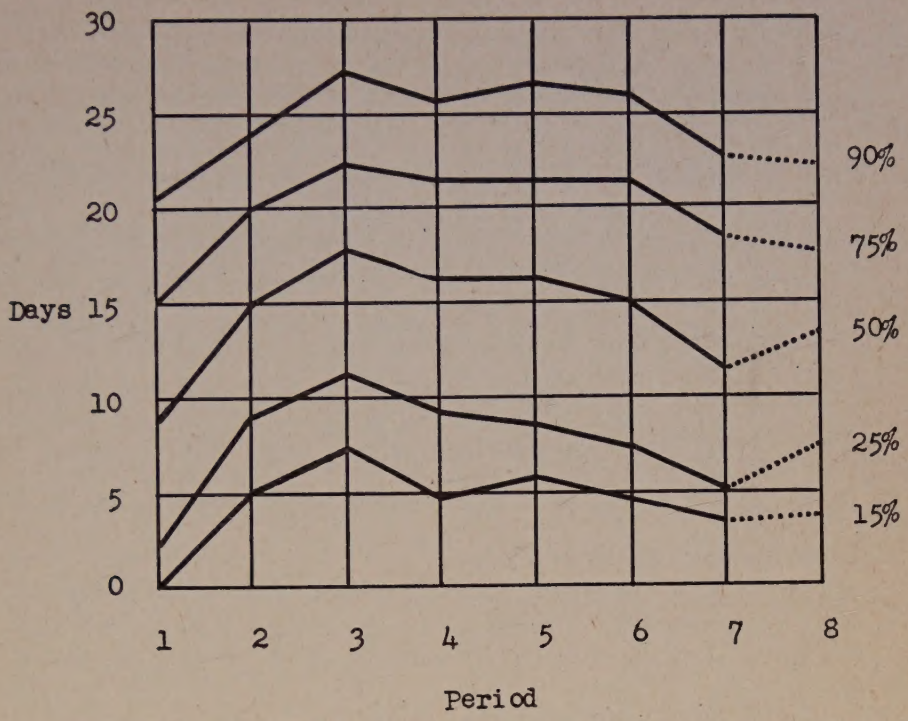

FIGURE 6. Spring codling moth emergence, five-year average from band-collected larvae. Number of days based at zero. Dotted sections are average of three years.

The record crop of 1943 was reflected in an increase in larvae but not an increase in the percentage of larvae to fruits. The similarity of the percentage of larvae to fruits for the four years 1942-1945 would seem to indicate less favourable conditions for codling moth than in 1941.

Varietal Differences

Ontario is a biennial bearer and its "off" years were 1942 and 1944. It so happened that McIntosh also carried a smaller crop in these years. Of the total crop McIntosh produced 62 per cent (range over the five years 56-67 per cent) and Ontario 38 per cent (range 33-44 per cent). Of the total larvae McIntosh contributed 61 per cent (range 56.5-71 per cent) and Ontario 39 per cent (range 29-46 per cent). Thus there would seem to be little difference in the numerical relationship of larvae to fruits in these two varieties.

Relation of Numbers of Larvae to Numbers of Wormy Fruits

It was known that not all wormy apples would give rise to mature larvae, that a single fruit may produce more than one larva (especially if the larvae are not contemporaneous), and that larvae in all stages of development can, and do, migrate from one apple to another. Nevertheless, it was hoped that by making a careful count of all wormy apples a comparison of the figures with numbers of larvae trapped would give some indication of the effectiveness of the bands, but the ratios obtained varied

so greatly that no reliance could be placed in them with regard to band efficacy. Actually the average percentage of mature larvae to apples with deep injuries for the ten trees over the five years was 26, with a range of 12.3 to 86.6, as shown in Table 3.

TABLE 3.—PERCENTAGE OF TRAPPED CODLING MOTH LARVAE TO WORMY FRUITS

Average and range of five trees in each variety

Year	McIntosh		Ontario		Average both varieties
	Average	Range	Average	Range	
1941	55.7	41.2–74.4	43.2	26.1–86.6	50.4
1942	17.5	13.8–20.0	18.2	12.4–26.9	17.8
1943	17.8	12.3–34.5	24.9	16.3–40.0	20.3
1944	18.7	16.1–23.2	17.3	14.0–28.5	18.2
1945	23.6	17.7–37.6	27.8	17.8–55.8	25.4

Period of Maturing Larvae

Over the five years larvae were taken from June 28 to November, though there were but few after the middle of October. With the exception of 1945 larvae were taken at every examination from the time the earliest were collected until about the middle of October. In 1945 there was one zero collection a few days after the earliest one. It was not possible to delimit first and second generation larvae.

TABLE 4.—TIME OF MATURITY OF CODLING MOTH LARVAE

Year	First larvae	Highest peak	No. larvae at peak
1941	June 28	August 24-25	232
1942	July 8	July 28-29	78
1943	July 7	September 14-15	209
1944	July 4	August 13-14	122
1945	July 13	August 20-21	247

Parasitism by Ascogaster

Larvae parasitized by Ascogaster are smaller, when mature, than normal larvae, and were separated from the latter as each collection was made. In spite of their small size these larvae must travel considerable distances at times, as some were taken in a trunk band on a tree that bore no fruit and therefore must have covered the distance from nearby trees. It is possible, however, that a trunk band may give too low a figure for parasitism. The only evidence for this, in the present study, is that the multiple-banded tree mentioned above had a parasitism of 19.9 per cent whereas the highest figure for any of the other five McIntosh trees, in the same year and with trunk bands only, was 17.1 per cent, and the average for these five trees 13.7 per cent. By coincidence the parasitism from the trunk band alone, on the multiple-banded tree, was 13.6 per cent.

Parasitized larvae were taken with the first collection (1941, 1944) or a few days later (1942, 1943, 1945) and from then on continuously to the end of the season or very nearly so. The percentage parasitism for each year is given in the table below.

TABLE 5.—PERCENTAGE OF CODLING MOTH LARVAE PARASITIZED BY *Ascogaster*

Year	McIntosh	Ontario	Both varieties
1941	13.7	24.1	17.5
1942	17.8	20.6	18.9
1943	15.2	28.8	19.8
1944	37.4	38.6	37.8
1945	23.6	14.3	19.3
All five years	19.3	23.6	21.0

The sudden increase in 1944 was not a natural one but was due to extraneous adults flying in from a point about 150 feet east of the orchard where thousands of adult *Ascogaster* collected elsewhere in the district, were released during the forepart of the season. The rise in 1944 is therefore readily explained but it is not at all clear why, in 1945, the gain of the previous season was almost entirely lost. The most important factor limiting *Ascogaster* seems to be secondary parasites of the chalcid genus *Perilampus*, as shown by Boyce (1941). The spray program may also have had some effect. In this orchard copper fungicides were used in 1941-1943 and wettable sulphur in 1944 and 1945.

The five-year average parasitism of larvae from McIntosh ran 1.7 per cent below and from Ontario 2.6 per cent above the 21 per cent average for both varieties. In the four years 1941-1944 there seemed to be a distinct preference for the variety Ontario but in 1945 the position was reversed.

Transforming and Diapause Larvae

In determining the proportion of first generation larvae which transformed to adults the same season, all larvae in the collections up to and including that from which the last first generation moth emerged were considered as first generation, although as previously stated it is actually not possible to separate first and second generation field-collected larvae.

TABLE 6.—PERCENTAGE OF FIRST GENERATION CODLING MOTH LARVAE TRANSFORMING TO ADULTS THE SAME SEASON

Year	McIntosh	Ontario	Both varieties
1941	43.6	70.9	52.8
1942	56.7	56.3	56.5
1943	46.2	64.1	53.8
1944	47.2	52.6	48.4
1945	25.4	29.3	26.8

The variety Ontario which matures about a month later than McIntosh, produced a somewhat higher proportion of transforming larvae than McIntosh. In the four years 1941-1944 the average for both varieties was rather constant around 50 per cent but in 1945 fell to about half of this percentage. The average for the previous 8 years, for insectary-reared material, was 52 per cent.

In contrast with the great variation in other phases of codling moth life history, the date on which summer larvae stopped transforming was remarkably constant from year to year. Practically all the earliest larvae transformed the same season; the proportion transforming then gradually decreased until finally all maturing larvae went into diapause. The time after which only diapause larvae were produced fell on almost the same calendar date every year regardless of weather conditions. This date, August 24, was maintained with extremes of only plus or minus three days in the case of orchard-collected larvae, although those reared in the insectary on picked fruit showed somewhat greater variation.

By plotting the dates on which larvae matured against the percentage of those transforming, for the five years and for each variety, a freehand sigmoid curve was drawn from which Table 7 was constructed. Very little difference was found between one year and another or between the varieties McIntosh and Ontario. The greatest scatter was in the region of 80-100 per cent transforming.

TABLE 7.—PERCENTAGE OF CODLING MOTH LARVAE TRANSFORMING THE SAME SEASON

Dates larvae matured	% Transforming	Dates larvae matured	% Transforming
Up to July 20	100-90	Up to August 9	30
July 25	90	August 11	20
July 31	80	August 13	10
August 3	70	August 15	5
August 4	60	August 19	2
August 5	50	August 25	1
August 7	40	August 27	0

It will be noted that the steep part of the curve runs from about August 1-15 and involves a decrease of about 75 per cent in numbers of mature larvae transforming. Thus if larvae are maturing in large numbers in this period a few days will make a great difference in the numbers of first generation moths. Furthermore, if large numbers of larvae mature before July 25, the second brood population of larvae will be a heavy one and, in an orchard of early and late varieties, the late varieties may ensure a large carry-over of larvae into the following year.

If we accept the idea that some stage in the development of the fruit influences the larvae feeding therein and induces diapause it is of interest to study the development of the fruit at the times the larvae appear to have been influenced. Some years earlier, measurements of Wealthy apples in the same orchard were taken at weekly intervals throughout the season. The number of apples per pound was plotted against time and the resulting curve resembled the positive half of a rectangular hyperbola.

This curve indicated that up to about June 23 growth was very rapid; that it then slowed down and by the middle of July over 90 per cent of the growth was completed. The growth curve of McIntosh and Ontario was estimated visually to be approximately the same. Now this growth curve had almost flattened out by about July 6 and larvae entering fruit at that time would be maturing around July 20-25. The table above indicates that a few larvae maturing at this time go into diapause. Thus it might be stated that diapause begins at the time the fruit growth curve flattens out. Now it is reasonable to suppose that the change in the fruit which influences diapause does not occur suddenly but requires an appreciable time to develop. Also in order to be affected, the larvae require a minimum amount of the changed food or must have had it at some definite stage in their development, probably both. Thus few larvae would be affected at first but the number would rise rapidly with increase of food change plus increase of numbers of larvae with more of their growth period coming under the influence of the change.

Heriot and Waddell (1942) found that a diet of immature seeds or pulp brought about a more rapid larval development than mature seeds or pulp and that a higher percentage of larvae entered diapause when fed on immature pulp as compared with other diets tried. The last finding is puzzling and appears to be negatived in the orchard, but other factors are doubtless involved. Krotkov (1941) working with McIntosh apples at Kingston, Ontario, found no starch present in apples picked on June 28. On July 6 the first traces of starch were observed; and from July 11 until August 8 there was an abundance of starch in cortex and pith. The idea that starch might be a factor in bringing about diapause is rather upset by the further statement of Krotkov that from August 15 there began a continuous decrease in the starch content until apples examined on October 12 either had no starch at all or mere traces. However, the starch is converted into sugars, and the actual factor may be the content of total digestible carbohydrates, either starch or sugar. Perhaps late in the season night temperatures may begin to have some effect. Incidentally, Krotkov's curve showing changes in respiration of apples through the growing season very closely approximates, except at the very end of the season, the growth curve obtained by plotting apples per pound against time.

As previously mentioned the widest variations in the curve of percentage transforming larvae occurred at the beginning—between 80-100 per cent transforming. This is what might be expected for the following reasons: (1) on the threshold of food-change all larvae are not likely to be affected alike; (2) all fruits on a tree may not change at exactly the same time; (3) the heredity factor may exert an influence on borderline cases; (4) casualties to larvae transforming would be in a higher ratio at this time (since these predominate) and therefore of more influence upon the results.

Prepupal Period of First Generation Larvae

No direct information on the duration of the prepupal period (*i.e.*, between cocooning and pupation) could be gained from the experiment under discussion but it is of interest to note that no pupae were found during the five years in any band examined every other day.

First Generation Moths

Over the five years first generation moths emerged as shown in Table 8.

TABLE 8.—EMERGENCE OF FIRST GENERATION MOTHS

Year	First moth	Highest peak	Last moth
1941	July 16	July 23	September 21
1942	July 27	August 12	September 5
1943	July 24	August 16	September 23
1944	July 19	August 4	September 17
1945	August 2	August 14	September 10

If the above dates are reasonably near those existing under natural conditions in the orchard, it would indicate that spray protection through most of August would be necessary where first brood is not well controlled.

The emergence of first generation moths is quite different from the spring brood in that the former practically all emerge over a period of about five days from the time the first moth, from any group of larvae maturing on the same date, emerges; the latter take several times as long. A compilation of data from approximately 4300 moths over the five-year period is given below. No significant difference was found between larvae collected from McIntosh and Ontario varieties.

TABLE 9.—AVERAGE EMERGENCE OF CODLING MOTHS FROM LARVAE MATURING ON ONE DAY

Emergence period (days)	% Emerging
1st	13
2nd	30
3rd	31
4th	17
5th	5
First five days	96

Declining emergence may continue until the thirteenth day though this has never happened in any one year (taking McIntosh and Ontario separately) without gaps on other days. Records then show a gap until the seventeenth day when one moth emerged in the five years. Likewise there was a single moth on the eighteenth, two on the twentieth, one on the twenty-second and one on the twenty-fourth day. These few moths came from larvae which appear to have been on the borderline between transformation and diapause, and their scarcity is a point of interest.

Winter Mortality

The figures on winter mortality given in Table 10 refer to the material in jars in the insectary under rather artificial conditions. The number of larvae (unparasitized) collected in one season minus the number of moths

TABLE 10.—WINTER MORTALITY OF CODLING MOTH LARVAE IN INSECTARY

Winter	Percentage mortality	Winter	Percentage mortality
1941-42	15	1944-45	33
1942-43	36	1945-46	21
1943-44	16		

emerging that same season was used as the number of carry-over larvae and compared with the count of spring brood moths.

No mortality differences were found between larvae from Ontario and McIntosh varieties.

Spring Brood Moth Emergence

Daily records were taken of the moth emergence in the insectary and Table 11 gives a brief summary of the emergence periods.

TABLE 11.—SPRING BROOD CODLING MOTH EMERGENCE IN INSECTARY

Year	First	25%	50%	75%	90%	Last
1942	June 4	June 13	June 25	June 30	July 5	July 26
1943	June 13	June 20	June 28	July 7	July 12	July 23
1944	June 5	June 22	June 29	July 5	July 7	July 28
1945	June 16	June 30	July 5	July 9	July 17	Aug. 6
1946	June 12	July 1	July 8	July 11	July 16	Aug. 9

To what extent does this insectary emergence compare with that of the orchard? Since the sun was not allowed to shine directly on the jars but would most certainly shine on some cocooning quarters in the orchard it was to be expected that some moths would emerge earlier in the orchard. Table 12 clearly shows this. The presence of first orchard moths was proved by the finding of empty pupal cases.

TABLE 12.—FIRST EMERGENCE OF CODLING MOTHS IN ORCHARD

Year	Date	Days earlier than insectary emergence
1942	May 29	6
1943	June 3	10
1944	May 27	9
1945	May 26	21
1946	May 28	15

There was therefore a lag in first emergence in the insectary of from 6 (1942) to 21 (1945) days. To judge by a comparison of insectary moth emergence and orchard fruit entries there appears to have been a fairly close relationship between main moth emergence in orchard and insectary for the years

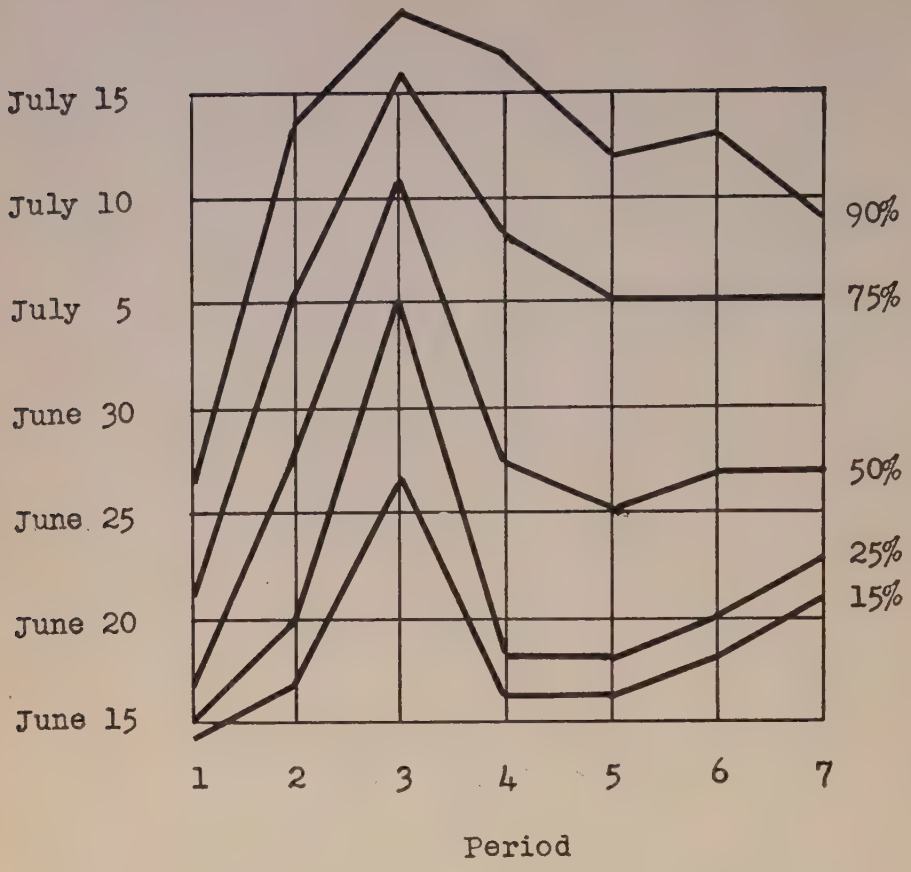

FIGURE 7. Emergence of codling moths in 1943 from larvae reared in insectary on picked fruit in 1942.

1942-1944 and a lag of several days for insectary emergence in 1945. The situation is complicated by a factor discussed below. Spring moths emerging in the comparatively equable insectary conditions did so in an order which bore some relation to the date the larvae matured the previous season. No doubt this happens also in the orchard but it is certain to be modified by the position of the larvae in the tree, e.g. north or south side, upper or lower side of inclined limbs, etc.

The period of emergence from the first to last moth varied from 40 days in 1943 to 58 days in 1946 with an average of 51 days for the five years. In the ten years 1931-1940, when larvae were held in glass vials pocketed in canvas bands wound spirally around pear trunks in a warm location, the maximum period of emergence was 61 days and the first moths emerged May 13 to May 30 with an average date of May 24. However, first entries were not found earlier during the 1931-1940 period than in the five years treated here and vial band moth emergence was probably earlier than in the orchard.

Spring Moth Emergence Related to Time of Larval Maturity

Since larvae were collected every other day (except at the close of the season) and each collection kept separate, and as moth emergence was noted daily, data became available to show the relationship between time of maturity and date of emergence the following spring. A simple analysis was made by lumping the numbers of larvae collected over a week or ten days into a group and thus arranging the season's catch into 7 to 9 chronological groups. The spring moth emergence from each of these groups was plotted at five levels, 15, 25, 50, 75, and 90 per cent, the figure in each case being the percentage of the total emergence of that particular group. The results are given below in tabular form and graphically in Figures 1-5. In comparing the graphs it should be noted that the groups or periods 1-9 do not always represent exactly the same dates from year to year.

There was a general tendency for the earliest moths to come from the earliest group of maturing larvae and for moths from groups 2, 3 or 4 to emerge progressively later. This was followed by a period of inconsistency in which moths from later groups began emerging earlier again or remained at a more or less stationary level. The last groups generally gave rise to moths only slightly later than the first group but 1942 was a very marked exception to this.

In Table 14 and Figure 6 the emergence for the five-year period has been averaged. It shows that at any given level of emergence, the group with the earliest average emergence was approximately a week earlier than the group with the latest average emergence. These groups were respectively 1 and 3, collected 21-30 days apart. Table 15 and Figure 7 show the emergence from larvae reared in the insectary on picked Wealthy apples. In this case also, emergence from group 1 larvae was earliest and from group 3 latest, but the difference was approximately 25 days.

It would appear from a comparison of Figures 1-5 that no simple cause for the relationship shown can be assigned. No doubt many interacting factors are at work such as heredity, food supply, rate of development of larvae, time required for rest period, diapause and how induced, and weather prevailing at critical times.

In 1943-46 (Figures 2-5) the latest moths came from larval groups 3 to 5 and it is just possible there may be a connection between this and the condition found by Armstrong (1945) in a pear orchard where moths emerged late. Armstrong suggested that as the pear fruit was too hard for larval penetration early in the season, survival would come only from later emerging moths and thus a late strain had become segregated in the orchard. The larvae from the Bartlett pears would be maturing at approximately the same period as those from apple which produced late emerging moths in the present study. Also very few very late maturing larvae would be produced in the pear orchard to give rise to early moths as they did in 1943 and 1944 in the apple orchard. However, it must be noted that Armstrong compared his pear larvae with apple larvae maturing on the same dates.

TABLE 13.—SPRING BROOD CODLING MOTH EMERGENCE FROM BAND-COLLECTED LARVAE

Emergence of moths in 1942 from larvae collected in 1941

Group No.	Period collected (1941)		No. moths	Dates (1942) given percentages had emerged				
	From	To		15%	25%	50%	75%	90%
1	26/7	5/8	214	June 8	June 9	June 12	June 22	June 29
2	7/8	13/8	510	June 14	June 22	June 27	July 1	July 5
3	15/8	21/8	793	June 11	June 19	June 28	July 1	July 7
4	23/8	29/8	1041	June 8	June 10	June 21	June 29	July 4
5	31/8	4/9	599	June 10	June 11	June 23	June 29	July 3
6	8/9	14/9	633	June 10	June 12	June 23	June 29	July 4
7	16/9	22/9	972	June 9	June 11	June 22	June 28	July 2
8	26/9	2/10	698	June 17	June 21	June 27	June 30	July 5
9	4/10	14/11	408	June 22	June 25	June 29	July 3	July 8

Emergence of moths in 1943 from larvae collected in 1942

1	29/7	4/8	60	June 15	June 16	June 25	June 27	July 5
2	6/8	12/8	117	June 16	June 17	June 26	July 3	July 6
3	14/8	20/8	156	June 21	June 25	June 30	July 7	July 11
4	22/8	28/8	155	June 18	June 23	July 3	July 8	July 12
5	30/8	5/9	117	June 17	June 19	July 3	July 8	July 14
6	7/9	13/9	134	June 16	June 18	June 27	July 8	July 13
7	15/9	21/9	96	June 18	June 20	June 27	July 6	July 10
8	23/9	30/9	30	June 16	June 20	June 26	July 2	July 7

Emergence of moths in 1944 from larvae collected in 1943

1	27/7	8/8	80	June 12	June 15	June 23	July 1	July 4
2	10/8	20/8	381	June 18	June 25	June 29	July 4	July 7
3	22/8	1/9	546	June 22	June 27	July 4	July 6	July 8
4	3/9	13/9	711	June 16	June 23	July 1	July 6	July 8
5	15/9	25/9	907	June 18	June 25	July 1	July 5	July 8
6	27/9	7/10	685	June 16	June 22	June 28	July 4	July 7
7	9/10	17/10	566	June 13	June 15	June 23	June 30	July 5
8	1/11	18/11	235	June 13	June 14	June 20	June 26	July 2

Emergence of moths in 1945 from larvae collected in 1944

1	27/7	8/8	123	June 22	June 28	July 2	July 6	July 9
2	10/8	20/8	428	June 29	July 1	July 5	July 9	July 17
3	22/8	1/9	260	June 29	June 30	July 6	July 12	July 20
4	3/9	13/9	78	June 24	June 28	July 1	July 6	July 10
5	15/9	25/9	64	June 28	June 29	July 2	July 7	July 14
6	27/9	7/10	35	June 30	July 1	July 6	July 10	July 16
7	14/10	1/11	26	June 27	June 28	June 30	July 5	July 12

Emergence of moths in 1946 from larvae collected in 1945

1	26/7	9/8	112	June 17	June 19	June 28	July 4	July 8
2	11/8	19/8	437	June 22	June 27	July 2	July 7	July 9
3	21/8	29/8	889	June 28	June 30	July 6	July 10	July 14
4	31/8	8/9	834	July 2	July 6	July 10	July 13	July 19
5	10/9	19/9	345	June 30	July 4	July 9	July 13	July 19
6	22/9	30/9	162	June 25	June 29	July 5	July 10	July 14
7	4/10	6/11	139	June 23	June 26	June 30	July 6	July 9

TABLE 14.—SPRING BROOD CODLING MOTH EMERGENCE—FIVE-YEAR AVERAGE FROM BAND COLLECTED LARVAE

Group period	Number of days, based at zero, given percentages had emerged				
	15%	25%	50%	75%	90%
1	0.0	2.6	9.2	15.2	20.2
2	5.0	9.6	15.0	20.0	24.0
3	7.4	11.4	18.0	22.4	27.2
4	4.8	9.2	16.4	21.6	25.8
5	5.8	8.8	16.8	21.6	26.8
6	4.6	7.6	15.0	21.4	26.0
7	3.2	5.2	11.6	18.2	22.8
*8	3.7	7.6	13.5	17.9	22.2

* Average of 3 years.

TABLE 15.—EMERGENCE OF CODLING MOTHS IN 1943 FROM LARVAE REARED IN INSECTARY ON PICKED FRUIT IN 1942

Group No.	Period collected		No. moths	Dates given percentages had emerged				
	From	To		15%	25%	50%	75%	90%
1	9/7	23/7	114	June 14	June 15	June 17	June 21	June 26
2	24/7	6/8	402	June 17	June 20	June 28	July 6	July 14
3	7/8	20/8	400	June 27	July 5	July 11	July 16	July 19
4	21/8	2/9	224	June 16	June 18	June 27	July 8	July 17
5	3/9	16/9	289	June 16	June 18	June 25	July 5	July 12
6	17/9	3/10	189	June 18	June 20	June 27	July 5	July 13
7	4/10	30/10	97	June 21	June 23	June 27	July 5	July 9

Biennial Larvae

So few biennial larvae were encountered that little attempt was made to study them, but nevertheless they are of considerable interest. Late in the season the corrugated-paper rolls, in which larvae had overwintered and given rise to spring moths, were opened and examined in the three years recorded in Table 16. Since among the larvae originally collected some had transformed the same year, some died, a number failed to survive the winter, etc., it is difficult to get a figure which will represent the proportion of biennial larvae. In the table the number of surviving larvae consists of the number of spring moths plus the number of biennial larvae found at the end of the season and therefore does not consider winter mortality.

TABLE 16.—PERCENTAGE OF BIENNIAL CODLING MOTH LARVAE

Year	No. of surviving larvae	No. of biennial larvae	Percentage biennial
1944	4051	27	0.7
1945	1024	5	0.5
1946	2967	51	1.7

A single biennial larva was taken in the July 29 collection in 1945, while all others were from collections made August 14 to October 13. Of the 83 biennial larvae taken over the three years, the larval collections made up to August 30 yielded 29, September 1-15, 25, September 15-30, 21, and October 1-13, 8 larvae, the percentages being 35, 30, 25 and 10, respectively.

The biennial larvae collected in 1943 were, in 1944, all placed in a single jar in the insectary and the moth emergence noted in 1945. The 21 moths emerging therefrom did so over a period of 21 days, from June 17 to July 7. The data in Table 11 reveal that, in 1945, the first moth emerged on June 16 and that, by July 9, 75 per cent had emerged. Thus spring moths arising from biennial larvae appear to emerge earlier than those from annual larvae, although the numbers are too small to give more than a possible indication.

Of the factors producing biennial larvae (probably heredity, temperature and humidity) nothing definite has been gleaned. Larvae wintered outside, in corrugated pasteboard, were placed in a house refrigerator (at about 40° F.) in the spring and held there until fall. They were then wintered outside for the second winter and in the spring produced moths with very little mortality. In the spring of 1942 some larvae were placed in a soil cavity in order to find out how much moth emergence could be delayed by unfavourable conditions in the orchard. Two jars containing larvae in pasteboard rolls were placed in a vertically submerged 6-inch field tile in the shade of a tree in the orchard. A loose board protected the top of the tile. The humidity in the tile and jars was extremely high and it was feared the larvae would succumb under these conditions. The larval mortality in the lower jar was, however, only 24 per cent and in the upper jar 17 per cent. Of the 244 larvae in the lower jar, seven (or 3 per cent) proved to be biennial and produced moths the following year in the insectary. The conditions which may have been operating here to produce the high proportion of biennial larvae were lowered temperatures, high humidity and crowding of larvae. The upper jar containing 109 larvae did not produce any biennial larvae.

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RHIZOSPHERE STUDIES AND ASSOCIATED MICROBIOLOGICAL PHENOMENA IN RELATION TO STRAWBERRY ROOT ROT[1]

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In previous studies on strawberry root rot West and Hildebrand (26) showed that certain treatments, such as the incorporation of soybeans into root rot soil, the addition of carbohydrate or acetic acid, and soil sterilization "caused a striking reduction in the incidence of root rot and a drastic shift in the bacterial equilibrium of the soil." Katznelson and Chase (12) found that these treatments as well as the addition of starch, cellulose, and molasses, raised the "bacterial balance index" (28) and thereby presumably induced a healthier state in the soil with respect to strawberry roots (26); addition to soil of chopped susceptible strawberry plants (Premier) lowered this index. As no plants were used in these experiments, however, the results could not be assessed in terms of the actual condition of the soils treated. The experiments were later repeated and extended to include plants. The results of these experiments together with the results of studies on various microbiological phenomena associated with this disease are presented in this paper.

EXPERIMENTAL

Two soils were used; one ("healthy" soil) which had never borne strawberries; the other ("root rot" soil) which had been planted to strawberries and was considered to be infested. Each soil was thoroughly mixed, sieved, and adjusted to 60 per cent of its moisture holding capacity. Portions of each soil were then treated with a wide variety of amendments and used to fill triplicate 9-in. pots. These pots were kept in the greenhouse, and their soil moisture content was maintained by periodic watering and weighing. Although many treatments were used, only the more significant of these are presented, and, since the results in general were very similar for both soils used, only those for the "root rot" soil are given. The following are the treatments to be discussed:

Series	Treatment
1	Control "root rot" soil
2	3 per cent green susceptible strawberry plant tissue
3	2.5 per cent dried blood
4	2.5 per cent oat straw
5	Acetic acid to pH 4.0—4.5
6	Steam sterilization

The acetic acid was added to the water used to bring the soil to the required moisture content. Partial sterilization was accomplished by autoclaving the soil-filled pots for 5 hours at 15 lb. pressure.

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TABLE 1.—EFFECT OF SOIL TREATMENT ON DEGREE OF ROOT ROT, "BACTERIAL BALANCE INDEX," AND SOIL REACTION

Treatment	Degree of root rot[1]		"Bacterial Balance Index"				Soil reaction (pH)		
			Soil		Rhizosphere				
	100 days	220 days	100 days	220 days	100 days	220 days	30 days	100 days	220 days
Control soil	7	9	+15	+31	+10	+34	7.5	7.2	7.8
Strawberry tissue	5	7	+ 8	+26	+30	− 7	7.1	7.3	7.7
Dried blood	1	1	+39	+20	+30	+51	8.5	5.5	5.0
Oat straw	9	10	−14	+18	+24	+12	7.5	7.5	7.4
Acetic acid	2	3	+26	+40	+25	+32	6.5	6.8	6.9
Steam	2	6	+32	+44	+38	− 7	—	7.2	7.6

[1] Number of lesions and degree of root discoloration rated on a scale of 1 to 10.

Thirty days after treatment, soil samples were removed for analysis, and four Premier (susceptible) strawberry runners were struck in each pot. These runners were cut, before they had formed roots, from older plants in the field. They were held in place in the pots by means of wire basket hooks while the free ends were kept in jars of water or nutrient solution until the roots had become established in the soil. After 100 and 220 days, soil and plants were removed for analysis. The roots were examined macroscopically for root discoloration and lesions and microscopically for the presence of specific internal parasitic fungi. The roots were then plated in order to determine the numbers of bacteria, fungi and actinomycetes, according to accepted procedures (17, 22). Root fragments (with lesions where possible) were also plated on potato dextrose agar for evidence of the types of fungi intimately associated with the roots (9, 26) rather than existing at the root surface. All fungi developing from these root sections were isolated and identified as to genus. In addition, all colonies of fungi developing on plates used for counts were transferred and identified in order to determine if qualitative differences could be detected between the fungi in the rhizosphere of these plants and those in the soil more distant from the roots. Bacteria were also isolated and classified, by the method of West and Lochhead (28), according to their nutritional requirements.

Macroscopic and Microscopic Examination of Roots

The influence of soil treatment on roots of susceptible strawberry plants is shown in Table 1, which gives a root rot rating based on the extent of discoloration of the roots and the number of lesions, and in Figure 1, which illustrates the effects obtained. Discoloration was most severe and lesions most abundant on roots in soil to which oat straw was added and, as was expected, in the control soil. Susceptible strawberry tissue did not appear to aggravate the root rot condition in the root rot soil, although it induced it in the healthy soil. The most effective treatments contributing to the control of this disease were, in order of efficiency, dried blood, acetic acid, and steam sterilization.

FIGURE 1. Effect of soil treatment on strawberry roots. 1. Control. 2. Oat straw. 3. Dried blood. 4. Acetic acid. 5. Steam sterilization.

TABLE 2.—INFLUENCE OF SOIL TREATMENT ON NUMBERS OF FUNGI BACTERIA AND ACTINOMYCETES IN ROOT ROT SOIL AND IN STRAWBERRY RHIZOSPHERES

Treatment	Soil			Rhizosphere		Rhizosphere: Soil	
	30 days	100 days	220 days	100 days	220 days	100 days	220 days
			Fungi (thousands per gram)				
Control soil	1.6	1.6	1.5	70	20	44	13
Strawberry tissue	1.8	3.3	2.6	270	490	82	190
Dried blood	0.06	0.4	5.1	700	1300	1750	255
Oat straw	14.0	6.0	3.0	110	100	18	33
Acetic acid	350.0	97.0	38.0	420	280	4	7
Steam	—	2.3	1.2	50	30	22	25
			Bacteria (ten-millions per gram)				
Control soil	5.4	2.6	5.8	270	180	104	31
Strawberry tissue	9.0	2.7	4.2	330	270	122	64
Dried blood	120.0	19.2	21.9	650	400	34	18
Oat straw	28.6	11.5	29.3	670	750	58	26
Acetic acid	11.2	7.1	9.2	180	50	25	5
Steam	—	11.8	22.8	500	300	42	13
			Actinomycetes (millions per gram)				
Control soil	5.0	2.3	1.0	100	150	45	150
Strawberry tissue	14.0	2.1	4.5	110	170	52	38
Dried blood	5.0	0.3	<0.1	<1	10	<1	100
Oat straw	15.0	1.6	3.0	40	850	25	283
Acetic acid	5.0	1.6	3.0	60	50	38	17
Steam	—	1.0	5.0	70	150	70	30

At 100 days from treatment, roots of healthy plants were free from phytopathogenic fungi frequently associated with strawberry root rot (*Rhizoctonia Solani*, *Cylindrocladium*, *Cylindrocarpon* (24, 26)), as was indicated by microscopic examination of stained root sections. These fungi began to invade roots more abundantly with time, and at 220 days most roots, except those in soil treated with dried blood, showed evidence of infection by one or more of these fungi. *Asterocystis* and a "mycorrhizal" fungus were common in most roots.

Microbiological Studies

Quantitative.—A summary of the results of counts of fungi, bacteria and actinomycetes is given in Table 2. Numbers of fungi were greatest in the soil treated with acetic acid and were markedly repressed for a time by dried blood, presumably due to the prevailing alkalinity of this soil as a result of rapid ammonification of the protein (Table 1). With time the reaction of this soil became acidic and an increase in fungi occurred. A "rhizosphere effect" was manifested by greater numbers of fungi in all root samples than in corresponding soil samples and especially by roots in soils treated with dried blood, acetic acid and strawberry tissue. Of particular interest in this connection was the "rhizosphere effect" of plants in soil treated with dried blood; their roots appeared to exert a protective

action on fungi, as there were considerably larger numbers of these organisms in the rhizosphere of these plants than in that of plants growing in the control soil, whereas the numbers in the corresponding soils showed a reverse effect at 100 days. Roots from soils treated with steam, oat straw or acetic acid did not appear to exert as strong a "rhizosphere effect" as those from soils treated with dried blood or strawberry tissue.

All treatments except strawberry tissue increased the number of bacteria in the soil, dried blood and oat straw being particularly effective. Again a "rhizosphere effect" was evident but all treatments, with the exception of strawberry tissue, reduced the rhizosphere: soil ratios. These ratios decreased, in general, in pots with the lowest disease incidence, confirming the observations of Hildebrand and West (9).

Actinomycetes also showed a response to treatment, especially in the soil 30 days after treatment, and a distinct "rhizosphere effect." Their suppression by dried blood after 100 days is likely due to the acid reaction in this soil at this and the following sampling periods. Again, as with fungi, the root zone became a more congenial habitat for these organisms as this soil became increasingly inimical. For example, at 220 days numbers of actinomycetes were very low ($<100,000$) in the soil but were appreciable in the rhizosphere, a ratio of 100 being obtained. Straw was very effective in stimulating these organisms in the soil at 30 days and in the rhizosphere at 220 days. The remaining treatments were not so stimulatory and tended to depress the rhizosphere: soil ratios at 220 days.

Qualitative-Bacteria.—The influence of soil treatments on the equilibrium between specific nutritional groups of soil bacteria, as expressed by the "bacterial balance index" (28), is shown by the data in Table 1. At 100 days, strawberry tissue, and oat straw in particular, had lowered the index in the soil, whereas the remaining treatments had increased it above that of the control. This effect was, in general, correlated with incidence of root rot; dried blood, with the highest index, supported the best root system, whereas oat straw, with the lowest index, had the most severely affected roots. The indices of the rhizosphere at this sampling period, while higher with all treatments than in the control soil, also tended to reflect the observed diseased condition of the roots (Figure 2). At 220 days, the "bacterial balance index" of all the soils, with the exception of that treated with dried blood, had increased, but no consistent effect of treatment was evident. Some correlation between index, treatments, and root rot condition is, however, apparent, in the rhizosphere indices (with one inexplicable exception—the index of the control soil itself). It may be noted that dried blood, giving an index of + 51, was the most effective treatment in relation to control of the disease; on the other hand, strawberry tissue, oat straw, and even steam treatment, yielded poor root systems at this time, a condition reflected by low indices. It is clear that, on the whole, correlation between treatment, degree of root rot, and the "bacterial balance index" is not as consistent as may be desired. Of course, the treatments were applied only once in these experiments whereas, in those reported by Hildebrand and West (9), as many as nine applications were involved; this factor would certainly result in conditions favorable for the development of a specific antagonistic or beneficial microflora and a more constant and reproducible effect.

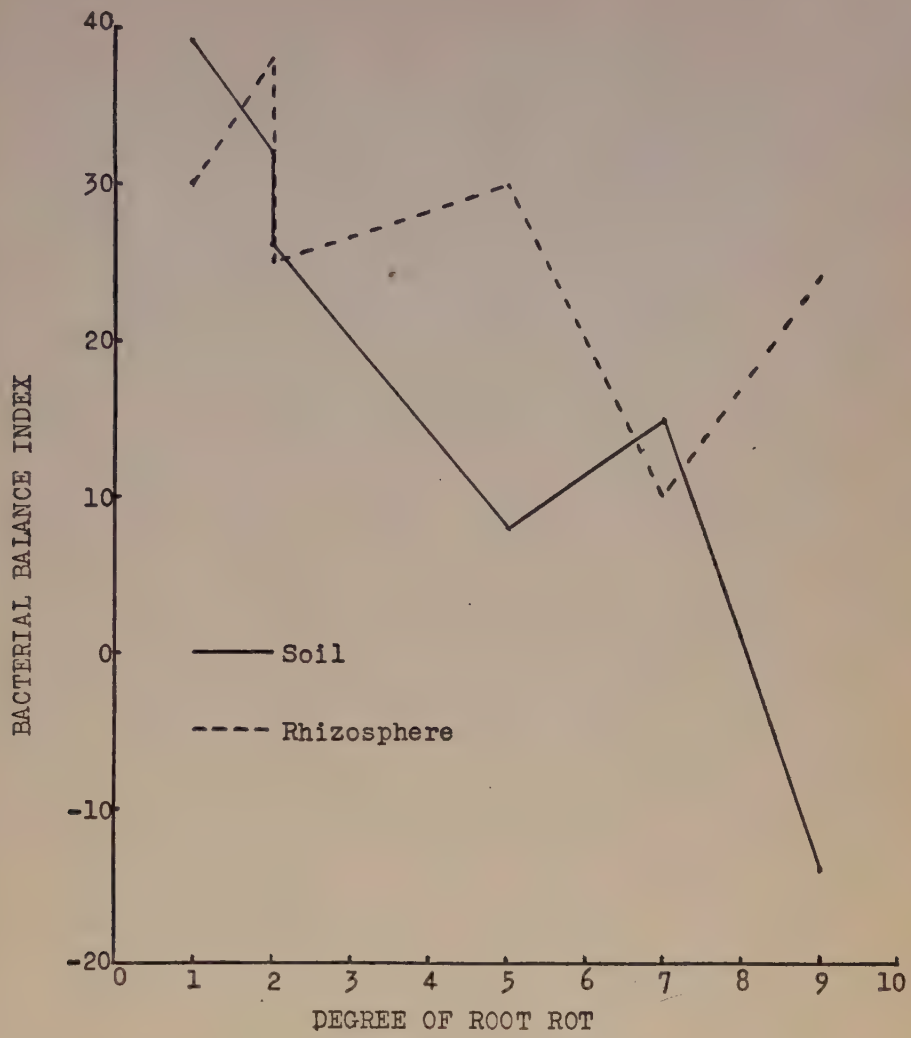

FIGURE 2. Relation between degree of root rot of strawberry plants and the Bacterial Balance Index of their rhizospheres and of the treated soils in which the plants were grown; 100 days after treatment.

The most striking effect of treatment on bacteria capable of growing in a simple inorganic medium (medium B of West and Lochhead (28)) is apparent in the reduced numbers of these organisms in soil treated with dried blood, and in the rhizosphere of plants growing in it, and the temporarily increased number in soil treated with oat straw (Table 3). At 220 days, the largest numbers of these organisms were found in the soil treated with strawberry tissue and in the rhizosphere of plants growing in it, and on roots in the soils treated with oat straw and with steam. Particularly noteworthy is the repeated observation (13, 18, 27) of relatively higher numbers of these organisms in the rhizosphere than in the corresponding soil (especially at 220 days). Straw appeared to reverse this effect at 100 days. Treatment did not appreciably stimulate bacteria requiring amino

TABLE 3.—PERCENTAGE INCIDENCE OF CERTAIN NUTRITIONAL GROUPS OF BACTERIA IN SOIL AND IN STRAWBERRY RHIZOSPHERES AS AFFECTED BY VARIOUS SOIL TREATMENTS

Soil treatment	Organisms growing well in medium B[1]				Requiring known amino acids for good growth[2]				Requiring complex factors in yeast and soil extracts			
	100 days		220 days		100 days		220 days		100 days		220 days	
	Soil	Rhiz.	Soil	Rhiz.	Soil	Rhiz.	Soil	Rhiz.	Soil	Rhiz.	Soil	Rhiz.
Control soil	19	20	5	14	12	28	33	23	52	32	52	34
Strawberry tissue	12	11	23	31	12	22	34	22	62	42	27	36
Dried blood	0	9	0	3	19	31	15	29	60	52	81	38
Oat straw	42	18	7	23	10	27	22	27	36	28	5	22
Acetic acid	11	22	3	8	17	15	10	18	57	46	48	32
Steam	11	17	0	38	17	16	20	10	49	31	53	24

[1] Inorganic salts—glucose medium; groups included are 1, 2, 3 of West and Lochhead (28).
[2] Groups 4, 5, 6, 7 (28).

acids. Again the observed "rhizosphere effect (13, 18, 27) on this group of bacteria may be noted in most cases at 100 days. A reversal occurs with some treatments at 220 days. Since no apparent influence of treatment on organisms requiring known growth factors was evident, these results were omitted. Bacteria requiring complex unidentified elements in yeast and soil extracts were uniformly more abundant (relatively) in the soil than in the corresponding rhizospheres at 100 days. At 220 days a reversal occurred in strawberry tissue and oat straw. This did not occur with oat straw in the other ("healthy") soil used in this investigation and may represent an error in determination. However, the reversal with strawberry tissue occurred in both soils. The numbers of these bacteria (81 per cent of the isolates) where dried blood was used was also characteristic of both soils treated.

Qualitative-Fungi.—The procedure described by West and Hildebrand (26) was adopted to determine the nature of the fungus flora intimately associated with the roots of the strawberry plants used in the above experiments. Although representatives of many genera were isolated, only a few of the predominant types along with those considered to have pathogenic significance (1, 24, 26)—*Cylindrocladium*, *Cylindrocarpon*, and *Rhizoctonia* (Orchid and *Solani* types)—are listed in Table 4. It is quite obvious that by far the largest number of isolations of these forms were made from roots which were most severely discoloured and had the most numerous lesions. The clean, white, healthy roots from soil treated with dried blood and acetic acid yielded none of these "pathogenic" forms, but chiefly Penicillia and Fusaria. Roots from steam-sterilized soil yielded these "pathogenic" types only at 220 days, when, as the degree of root rot indicates, they appeared to be appreciably infected. *Rhizoctonia Solani* appeared to be the most frequently isolated fungus from suspected and infected roots.

Identifications of fungi were also made from representative plates used for making counts, to determine primarily whether or not a qualitative difference existed between fungi in the rhizosphere and fungi in the soil at a distance from the root. Very little has been done along this line, emphasis having been placed on bacterial groups. The fungi to be considered in

TABLE 4.—FUNGI ISOLATED FROM ROOT SECTIONS OF STRAWBERRY PLANTS GROWING IN DIFFERENTLY TREATED SOILS

Genus	Soil treatment											
	Control		Strawberry tissue		Dried blood		Oat straw		Acetic acid		Steam	
	100[1]	220	100	220	100	220	100	220	100	220	100	220
Cylindrocarpon	2[2]	23	7	7	—	—	—	7	—	—	—	—
Cylindrocladium	—	—	2	2	—	—	—	—	—	—	—	—
Rhizoctonia Solani	—	16	21	—	—	—	16	15	—	—	—	29
Rhizoctonia (Orchid)	35	—	21	7	—	—	—	—	—	—	—	4
Fusarium	42	7	21	—	55	3	2	30	6	10	67	2
Penicillium	13	5	19	23	34	68	56	11	38	71	27	16
Aspergillus	—	2	—	7	2	—	7	—	19	—	6	14
Trichoderma	2	—	—	—	—	—	14	2	—	2	—	8
Degree of root rot[3]	7	9	5	7	1	1	9	10	2	3	2	6

[1] Days.
[2] Per cent of total isolates.
[3] Number of lesions and degree of root discoloration rated on a scale of 1 to 10.

this section are the saprophytic forms, as numbers of "pathogenic" forms might be expected to be greatest in the immediate vicinity of (on and in) the root. Some evidence of such qualitative differences has been obtained in earlier investigations with flax and tomato plants (13, 23), and the results shown in Table 5 appear to support this view. In the control series, *Aspergillus*, *Fusarium* and dark green *Penicillium* types were isolated from the soil but were absent in the rhizosphere of roots growing in it; conversely, *Cladosporium*, *Chaetomium* and an unidentified non-sporulating fungus "C" were isolated from the rhizosphere plates but not from the soil plates. As might be expected, different treatments altered this picture. For example, rhizospheres in soil treated with strawberry tissue supported a red-green *Penicillium* (26 per cent), *Verticillium* (28 per cent), and *Cladosporium* (4 per cent), whereas the soils yielded none of these but contained *Aspergillus* (6 per cent), *Trichoderma* (12 per cent), *Mucor-Rhizopus* forms (6 per cent), *Oothecium* (12 per cent) and the unidentified fungus "C" (24 per cent). It would seem, therefore, that qualitative differences do exist between the fungi of the rhizosphere and those of the soil at a distance from the root.

Of equal interest is the change with time of the fungus flora of the rhizosphere. This may be observed in Table 4 and is even more clearly evident from the data summarized in Table 5. In every case, except with the acetic acid series, numbers of Penicillia increased with time. *Verticillium* appeared in most rhizospheres at 220 days, whereas *Cladosporium* was more abundant at 100 days (Table 5). Yeasts, *Fusarium*, and *Alternaria* species, where they occurred, appeared in most cases to be more numerous at 100 days.

Influence of Acetic Acid

The beneficial effect of acetic acid in the treatment of root rot soil was pointed out by West and Hildebrand (26) and has been corroborated in this investigation. This acid is known to be toxic to fungi and bacteria

TABLE 5.—DISTRIBUTION OF FUNGI IN SOIL AND IN STRAWBERRY RHIZOSPHERES AS AFFECTED BY SOIL TREATMENT AND TIME

Genus	Soil treatment																	
	Control			Strawberry tissue			Dried blood			Oat straw			Acetic acid			Steam		
	100[1]	220		100	220		100	220		100	220		100	220		100	220	
	Rhiz.	Soil	Rhiz.	Rhiz.	Soil	Rhiz.	Rhiz.	Soil	Rhiz.	Rhiz.	Soil	Rhiz.	Rhiz.	Soil	Rhiz.	Rhiz.	Soil	Rhiz.
Penicillium—total	16[2]	54	33	3	28	66	40	81	54	33	42	51	94	63	54	0	14	27
Green	—[3]	47	33	—	28	40	—	0	16	—	0	0	—	63	54	—	14	18
Red-green	—	0	0	—	0	26	—	0	0	—	14	4	—	0	0	—	0	0
Gray-green	—	0	0	—	0	0	—	60	38	—	28	18	—	0	0	—	0	0
Dark-green	—	17	0	—	0	0	—	0	0	—	0	11	—	0	0	—	0	0
Yellow	—	0	0	—	0	0	—	21	0	—	0	11	—	0	0	—	0	0
Gray	—	0	0	—	0	0	—	0	0	—	0	7	—	0	0	—	0	9
Aspergillus	0	6	0	3	6	0	0	0	0	0	0	4	0	0	0	63	0	0
Trichoderma	0	0	0	0	12	0	0	0	0	4	14	4	6	7	0	0	0	45
Verticillium	9	24	14	0	0	28	0	3	13	0	0	12	0	0	0	0	29	10
Cladosporium	16	0	10	27	0	4	50	3	33	18	14	4	0	0	0	31	0	0
Mucor-Rhizopus	0	0	0	0	6	0	0	0	0	0	0	0	0	10	5	0	0	18
Fusarium	0	6	0	1	6	0	0	0	0	7	0	0	0	0	0	6	0	0
Alternaria	0	0	0	1	0	0	0	0	0	7	0	0	0	0	0	0	0	0
Chaetomium	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oothecium	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0
Yeast	50	0	0	44	6	2	10	3	0	11	0	0	0	7	14	0	21	0
Unidentified "A"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	36	0
"B"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
"C"	9	0	17	21	24	0	0	10	0	20	30	25	0	13	18	0	0	0

[1] Days.
[2] Per cent of total isolates.
[3] Indicates that no differentiation was made among the Penicillia in the 100-day series.

(3, 10, 15, 16, 19) as a result, not only of its acidic nature, but also of the toxicity of the undissociated molecule (3, 29). It was considered of interest to determine its influence on specific organisms isolated from the rhizosphere of diseased plants ("pathogenic" and saprophytic fungi, and bacteria involved in computing the "bacterial balance index"). Varying amounts of acetic acid were added aseptically to appropriate quantities of media (Peptone-glucose for fungi, and medium Y of West and Lochhead (28) for bacteria) to give a range of pH from 6.9 to 3.6. In other tests, hydrochloric acid was substituted for acetic acid, the lowest pH used in this case being 2.0. The media were inoculated, incubated for a suitable period, and then examined. All bacteria were inhibited at pH 6.0, so that no differences could be detected between the effects of acetic and hydrochloric acids by the method used. The fungi tested and the results obtained are given in Table 6, but only those reactions (pH) that restricted and entirely suppressed growth are shown. It is apparent that acetic acid is the more toxic of the two acids. Of particular interest was the greater sensitivity—not only to low pH, but also to acetic acid—of fungi with "pathogenic" propensities, such as *Cylindrocladium*, *Cylindrocarpon* and *Rhizoctonia*. This influence of acetic acid may offer an explanation for the observed beneficial effects of the acid on strawberry plants in root rot soil.

TABLE 6.—INFLUENCE OF ACETIC ACID AND HYDROCHLORIC ACID AT DIFFERENT pH LEVELS ON VARIOUS FUNGI

Fungus	pH effect			
	Growth restricted		Growth entirely suppressed	
	Acetic acid	Hydrochloric acid	Acetic acid	Hydrochloric acid
Hormodendrum	4.0	—	3.8	—
Penicillium	4.0	2.5	3.8	<2.0
Aspergillus	3.8	<2.0	3.7	<2.0
Trichoderma	3.8	2.5	3.7	2.0
Fusarium 1.	4.4	2.5	3.7	2.0
Fusarium 2.	4.0	3.0	3.8	2.0
Pythium	4.2	—	4.0	—
Cylindrocladium 1.	>4.75	3.5	4.0	2.5
Cylindrocladium 2.	>4.75	3.5	4.0	2.5
Cylindrocarpon 1.	4.5	3.5	4.0	2.5
Cylindrocarpon 2.	4.5	4.0	4.0	3.0
Rhizoctonia Solani 1.	4.5	3.5	4.2	2.5
Rhizoctonia Solani 2.	4.5	4.0	4.4	3.0
Rhizoctonia (Orchid) 1.	4.5	3.5	4.0	3.0
Rhizoctonia (Orchid) 2.	—	3.5	—	3.0

TABLE 7.—EFFECT OF METABOLIC FILTRATES OF CERTAIN FUNGI ON STRAWBERRY SEEDLINGS[1]

Source of filtrate	pH original filtrate	Unacidified filtrate		Acidified filtrate (pH 4.6)	
		Leaves	Roots	Leaves	Roots
Rhizoctonia Solani	7.0	Unchanged	Unchanged	Unchanged	Unchanged
Rhizoctonia (Orchid)	7.0	Slightly wilted	Unchanged	Slightly wilted	Unchanged
Cylindrocladium	7.8	Wilted, dry	Slightly brown	Wilted, dry	Slightly brown
Cylindrocarpon	5.0	Unchanged	Slightly brown	One plant, dry	Slightly brown
Fusarium	7.8	Wilted, dry	Slightly brown	Wilted, dry	Slightly brown
Controls					
Potato dextrose	6.0	Unchanged	Slightly brown	Unchanged	Slightly brown
Tap water	5.8	Unchanged	Unchanged	Unchanged	Unchanged

[1] Fungi grown in a fluid medium for 4 weeks. Seedlings kept in metabolic solutions for 4 days.

Effect of Metabolic By-Products of "Pathogenic" Fungi

The use of metabolic products of specific fungi was also attempted in an effort to produce symptoms of the disease in strawberry roots, following the work of Gottlieb (6, 7) and Plattner and Clauson-Kaas (20) with a toxin produced by *Fusarium lycopersici* which caused wilt of tomato plants. The fungi were grown in potato dextrose fluid medium for various lengths of time at 28° C., after which the fungus mats were filtered off. The filtrates were then transferred to test tubes and roots of susceptible strawberry seedlings in duplicate were immersed in them. Bacterial growth frequently developed, as the reaction of the filtrates was usually near neutrality. Although this did not affect the results materially, the experiments were repeated and the filtrates divided into two portions; one portion was held as a control and the other was adjusted to pH 4.6, to prevent bacterial growth. Again the results were unaffected. In repeated trials it was found that filtrates of *Cylindrocladium* and *Fusarium* caused complete wilting of the seedlings within 3 or 4 days (Table 7). *Rhizoctonia Solani* and the "Orchid" type were ineffective and *Cylindrocarpon* only partly so. Control plants in water or potato dextrose medium remained virtually unchanged. No correlation, however, between root discoloration and wilting of the plants was evident.

The use of bacterial suspensions yielded no consistent or reproducible results, contrary to the observation of Hildebrand and West (9) in respect to browning of root sections by bacteria of group 3.

Inoculation Experiments

Inoculations were carried out with various combinations of saprophytic and "pathogenic" fungi and bacteria of the critical groups 3, 5, 7, 9. A mixture of the fungi listed in Table 5 constituted the "saprophyte" inoculum; the "pathogenic" types included *Cylindrocarpon*, *Cylindrocladium*, *Rhizoctonia* (*Solani* and "Orchid" type) and *Pythium*. Twenty isolates of group 3 bacteria and 20 of the other three groups were used. The fungi were introduced individually into sterile soil and incubated for two weeks; 100 grams of inoculum of each pathogen or 100 grams of a mixture of the five were used per pot. Soil inoculum of saprophytic fungi

TABLE 8.—EFFECT OF INOCULATING SOIL WITH VARIOUS ORGANISMS, ALONE AND IN COMBINATION, ON STRAWBERRY SEEDLINGS AFTER 4 WEEKS' GROWTH

Inoculum	Green weight of 3 plants (grams)	Degree root discoloration[1]	Number of isolations of original pathogen from 25 root sections	Microscopic examination of roots
Rhizoctonia Solani	0.52	4	22	*R. Solani* in most sections
" + Group 3 bacteria	0.83	4	23	
" + Groups 5, 7, 9 bacteria	0.48	6	24	
" + Saprophytic fungi	0.19	7	24	
Rhizoctonia "orchid"	1.84	3	3	*Rhizoctonia* and *Asterocystis* in most sections
" + Group 3 bacteria	2.07	2	2	
" + Groups 5, 7, 9 bacteria	1.70	2	3	
" + Saprophytic fungi	1.61	2	10	
Pythium sp.	1.34	4	23	*Pythium* in many sections
" + Group 3 bacteria	2.43	1	13	
" + Groups 5, 7, 9 bacteria	1.41	2	16	
" + Saprophytic fungi	0.57	4	24	
Cylindrocladium sp.	1.71	3	4	Little evidence of infection
" + Group 3 bacteria	1.73	1	2	
" + Groups 5, 7, 9 bacteria	1.85	2	1	
" + Saprophytic fungi	1.83	2	3	
Cylindrocarpon sp.	1.21	3	0	Little evidence of infection
" + Group 3 bacteria	1.70	2	0	
" + Groups 5, 7, 9 bacteria	2.02	1	1	
" + Saprophytic fungi	2.33	1	1	
Check (sterile soil)	2.50	1	0	Little evidence of infection

[1] Number of lesions and degree of root discoloration rated on a scale of 1 to 10.

was prepared in a similar manner, mixed, and 100 grams of each mixture used per pot. Bacteria were grown for 10 days in medium B (28) fortified with soil extract, and the cultures mixed (as indicated in Table 8). This fluid inoculum was used at the rate of 100 ml. per pot. Each pot contained 2 pounds of compost soil, which had been partially sterilized by steaming for 3 hours at 15 lb. The pots were allowed to stand in the greenhouse for 2 weeks, after which the inocula were added in triplicate. On the following day, 2 seedlings (6-weeks old), grown in sterile soil and possessing clean white roots, were planted in each pot. Four weeks later, representative plants were removed for macroscopic and microscopic examination and twenty-five root segments of each plated on acidified and non-acidified potato dextrose agar. Other plants were removed, washed thoroughly, dried between filter papers and weighed. Representative results with some of the more effective combinations of organisms (with respect to their influence on the plants) are given in Table 8. Reduction in plant weight and root discoloration were most pronounced in plants attacked by *Rhizoctonia Solani*. This organism was recovered from most of the root segments examined. *Pythium* sp. was also recovered frequently, but did not appear to induce such serious effects. The influence of bacteria was

TABLE 9.—EFFECT OF INOCULATING SOIL WITH VARIOUS FUNGI, ALONE AND IN COMBINATION, ON STRAWBERRY SEEDLINGS AFTER 3 MONTHS' GROWTH

Inoculum	Green weight of 3 plants (grams)	Degree root discoloration[1]	Number of isolates of pathogenic types	Microscopic examination of roots
Rhizoctonia Solani	3.5	6	16	*Rhizoctonia*
Rhizoctonia (orchid)	9.0	2	13	*Rhizoctonia*
Pythium	7.4	4	6	Few fungi
Cylindrocladium	13.6	1	4	Few fungi
Cylindrocarpon	11.5	2	0	Few fungi
Mixed pathogens	8.9	2	2	*Rhizoctonia*
"Pathogens" + saprophytes	13.5	2	8	*Rhizoctonia*
Check (sterile soil)	14.6	0	0	No fungi

[1] Number of lesions and degree of root discoloration rated on scale of 1 to 10.

negligible in all cases. After 3 months, the remaining plants were taken up and examined. The results are summarized in Table 9. Again *Rhizoctonia Solani* and *Pythium* are definitely implicated.

DISCUSSION

The influence of organic matter on the incidence of root rots of various plants has received considerable attention. Effects both beneficial and harmful have been reported (1, 2, 4, 5, 14, 21). However, the specific influence of the organic substances used is not very clear. Such substances may exert their effect by stimulating the soil microflora to the extent that it competes successfully for space, oxygen or food with the pathogen (14, 21), or they may stimulate such development of the plant as to enable it to resist or overcome infection (25). West and Hildebrand (26) have presented evidence that organic materials undergoing "a predominantly carbohydrate fermentation with the production of volatile organic acids" induce profound changes in the quantitative and qualitative bacterial and fungus populations in soils supporting strawberry plants, and in the rhizospheres of these plants, with a resulting diminution or actual elimination of the root rot factor. Katznelson and Chase (12) found that carbohydrates, such as starch, molasses and cellulose, inducted a "favourable condition" of the soil, as indicated by the "bacterial balance index" of West and Lochhead (28). They found, however, that the effect of treatment depended on the quantities of materials used and the period of decomposition. For example, 1 per cent dextrose gave an "index" of −25 at 40 days and +15 at 310, whereas 5 per cent dextrose gave figures of +7 and +29 for the respective sampling periods. The property of inducing a favourable condition in the soil from the point of view of root rot is, however, not restricted to carbohydrates. Dried blood was the most effective of the many substances used (not all of which were included in

the data presented). It exerted a striking and prolonged effect on the bacterial and fungus flora of both soil and rhizosphere, giving an index of + 51 in the latter at 220 days. The alkalinity resulting from the intense ammonification of this substance in the early stage of decomposition and/or the acid condition developing in the latter stages (perhaps due to nitrification) may both be responsible for the results obtained. The influence, on the causal organisms or on the plant, of readily available nitrogen must also be considered in this regard (14a). Further experience with this material has indicated, however, that care must be exercised in its use, as the plants themselves may suffer if introduced into the soil too soon after treatment.

The results of the experiments reported here suggest that fungi are the most important agents in regard to this root rot disease (8, 24). The reduction in numbers of fungi possessing "parasitic" capability by treatments that yielded healthy roots is very marked and completely in accord with the findings of West and Hildebrand (26). The frequency with which *Rhizoctonia Solani* was isolated from suspected root material suggests that this fungus is by far the most important of the "pathogens" tested. Bacteria of the "harmful" (group 3) type whether added to soil or tested in mixed fluid culture, did not seem to influence the development of a root-rot condition, as was suggested by Hildebrand and West (9). These bacteria may be secondary invaders that enter and develop on root tissues after these are penetrated by a primary invader, such as a fungus or possibly a nematode (8). Specific treatments may well stimulate or retard multiplication of these bacteria which may then function as an index of the effect of the treatment on the root-rot condition rather than be involved *per se* in its origin. Although striking effects were obtained with metabolic products of a species of *Fusarium* and of *Cylindrocladium*, more work is required to determine whether or not these organisms are pathogenic. On the whole, inoculation experiments failed to do this, although *Cylindrocladium* was isolated from some root sections obtained from soil inoculated with it (Table 8) and from naturally infected roots (Table 4). This fungus was able to penetrate healthy strawberry roots and cause browning of the tissue when agar colonies of it were placed directly on them.

The results of this study are of interest also from the standpoint of the more general problem of the "rhizosphere effect" of plants. Stimulation of fungus, bacteria and actinomycete numbers by roots is now a common observation. However, the marked "rhizosphere effect" exerted by roots on organisms which have been depressed in the adjacent soil by certain treatments is particularly interesting. This buffering effect of the root surfaces on numbers of fungi and actinomycetes occurred in soil receiving dried blood (Table 2). A similar phenomenon, with the same groups of organisms, was observed in tomato plants (13) growing in steam sterilized soil. This effect may possibly be explained by stimulation of plant growth by the treatment, resulting in more vigorous excretion and consequent increase in the rhizosphere population (11). On the other hand, certain treatments may produce conditions unfavourable for the plant, with the result that the "rhizosphere effect," though demonstrable, is diminished. This occurred, for example, with rhizospheres in acetic acid treated soil, as indicated by a depression of the rhizosphere: soil

ratios of fungi and actinomycetes below those of the control (Table 2). Most of the treatments also reduced the rhizosphere: soil ratios of bacteria. Similar effects have been demonstrated with tomato rhizospheres (13).

The observed tendencies for bacteria with complex nutritional requirements to be relatively more abundant in soil than on root surfaces, and of bacteria with simple nutritional needs and those with requirements for amino acids to be relatively more numerous on root surfaces, have been recorded previously for a variety of plants (13, 18, 27). As yet adequate explanation for these effects is lacking. Associative and antagonistic phenomena may play an important role in this root zone as pointed out by Lochhead and Thexton (18), who showed that filtrates of bacteria with very simple nutritional requirements stimulated certain bacteria requiring amino acids, but repressed others requiring known vitamins.

The selective action of roots on soil fungi has received little attention. Timonin (23), working with flax, reported that, of 19 genera isolated from soil and rhizosphere, 10 were obtained from the latter only. The resistance and susceptibility of these plants to disease and the moisture content of the soil were found to affect this distribution. Katznelson and Richardson (13) also obtained differences between the fungus flora of the rhizospheres of tomato plants and of the corresponding soil. This selective action of roots, especially as affected by soil treatment, was again demonstrated with strawberry plants. It was also shown that this flora (as is the case with other groups of organisms) was far from stable and changed with time, probably in response to the influence of the stage of growth of the plant.

The over-all picture one obtains of the rhizosphere is that of a complex of micro-organisms, some harmless, others beneficial, and still others with pathogenic propensities, in equilibrium but susceptible to the influence of various factors, such as moisture, soil treatment and nature and age of the plant. By controlling the direction of change of this equilibrium and the intensity of microbial activity in the root zone by means of appropriate soil amendments, it appears to be possible to control certain root diseases. The influence of these treatments on the nutrition and vigour of the plant itself may also be an important factor contributing to its resistance to disease (25).

SUMMARY

Treatment of soil infested with strawberry root rot with dried blood, acetic acid and by steam sterilization resulted in the reduction of the disease factor and the development of clean, healthy roots. Oat straw appeared to increase the severity of the disease.

Healthy roots were free from fungi frequently associated with the disease, such as *Rhizoctonia Solani*, *Cylindrocarpon*, *Cylindrocladium* and *Pythium*, whereas infected, discolored roots yielded these forms, particularly *Rhizoctonia Solani*.

Marked differences in numbers of fungi, bacteria and actinomycetes were observed in soils and rhizospheres as a result of treatment. In general rhizosphere: soil ratios for bacteria tended to decrease in pots with the lowest disease incidence.

Some positive correlation between degree of root rot and the "bacterial balance index" of soils and rhizospheres was obtained, particularly at the 100-day sampling period.

Organisms requiring complex nutritional factors were relatively more abundant in the soil than in the rhizosphere. Bacteria with very simple nutritional needs and those requiring amino acids for growth were, on the whole, relatively more numerous in the rhizosphere than in adjacent soil.

Qualitative differences between the fungus flora of the soil and that of the rhizosphere, and a change in the flora of the rhizosphere with time, were also observed.

Fungi were shown to be more sensitive to acetic than to hydrochloric acid at the same pH, with organisms of "pathogenic capability," such as *Cylindrocladium*, *Cylindrocarpon* and *Rhizoctonia*, more sensitive than common saprophytic fungi to acid reaction, particularly when induced by acetic acid.

Metabolic products of *Fusarium*, *Cylindrocladium* and, to some extent, of *Cylindrocarpon*, caused rapid wilting of strawberry seedlings.

Inoculation of sterilized soil with various combinations of saprophytic and "pathogenic" fungi and certain groups of bacteria indicated that *Rhizoctonia Solani* was the most serious of the pathogens used. It was capable of causing rapid discoloration of seedlings and was isolated from infected roots in about 90 per cent of the trials. *Pythium* sp. was capable of rapid penetration of strawberry roots.

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STUDY OF FERTILIZER UPTAKE USING RADIO-PHOSPHORUS: III

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INTRODUCTION

It is now well known that the radioactive tracer method can be profitably applied to numerous problems of interest to agriculture. Radiophosphorus, P^{32}, can be used in the study of phosphate fertilizer utilization and the general features of fertilizer uptake have already been reported (1), (2).

The present experiments were designed to show the variation in phosphorus uptake when phosphate fertilizer is applied at different rates. In addition, an attempt was made to determine the extent to which the fertilizer remaining after cropping once is available to a second crop. $NH_4H_2PO_4$ was used, the nitrogen and phosphorus content being similar to that of 11-48-0, ammonium phosphate (the principal phosphate fertilizer used in Saskatchewan).

GENERAL EXPERIMENTAL PROCEDURE

The following table outlines the experiments:

Table 1.—Experimental details

Series	Rate of fertilizer application lb./acre	Period of growth-weeks	No. of pots	$NH_4H_2PO_4$ applied, mg. of P. per pot	Radiophosphorus per pot counts/min. Apr. 15
1	0	6	6	0	0
2	25	6	6	18.1	1.6×10^7
3	75	6	6	54.3	1×10^6
4	225	6	4	162.9	1.6×10^7
5	0	8	6	0	0
6	25	8	6	18.1	1×10^6
7	75	8	6	54.3	1×10^6
8	Series 1 re-seeded	6	6	—	—
9	Series 2 re-seeded	6	6	—	—
10	Series 4 re-seeded	6	4	—	—

For the fertilized pots, a weighed quantity of $NH_4H_2PO_4$ was dissolved in water to which the P^{32} in the form of an aqueous solution of NaH_2PO_4 was added and the mixture made up to a definite volume. The weight of $NH_4H_2PO_4$ and counts per minute of P^{32} were so chosen that aliquots of the fertilizer solution gave each pot (glazed gallon crocks) of each series the quantities specified in Table 1. Several ml. of each solution remained and were placed in glass-stoppered bottles which were then sealed with paraffin wax. These solutions were used in preparing standards. By

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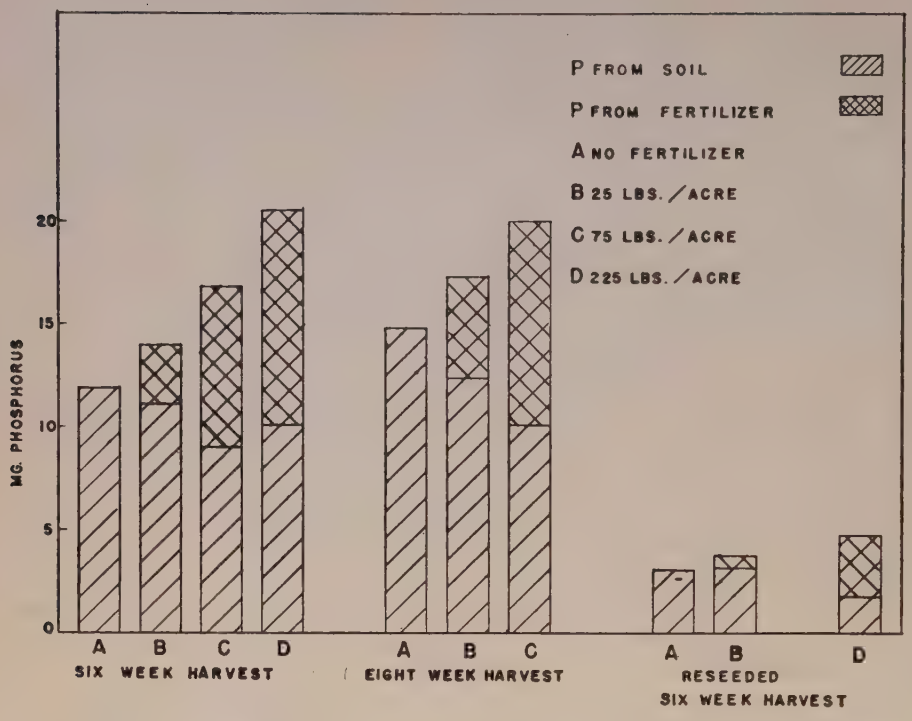

FIGURE 1. Uptake of soil phosphorus and fertilizer phosphorus for different rates of phosphate application.

counting the standard and the activity recovered from the ashed plant material, the per cent radiophosphorus taken up by the plant was easily calculated. Decay corrections and corrections for counter fluctuations were thus taken care of.

The soil used for the experiment was a solonetzic member of the Elstow Association having a silt loam texture (3). The soil was obtained from the farm of C. Agar, Floral, Sask., as in previous experiments (1, 2). An amount of soil equal to 3200 gm. of air dry soil was weighed into each pot. A two-inch depth of soil was removed from each pot, the seed and fertilizer were applied at this level and then covered with the two inches of soil. Five Thatcher wheat seeds were sown in each pot. When the seedlings emerged, the number in excess of three was removed.

The experiment was started April 15 in the greenhouse, and the plants grew well. Harvesting took place at six and eight weeks, just after heading and at the hard dough stage, respectively. Series 1, 2 and 4, that is, the pots fertilized at 0, 25, and 225 lb./acre, were re-seeded immediately after the six-week harvest. This second crop grew under much higher temperatures than the first crop, and consequently no tillering took place, the plants were weaker and the heads much smaller than for the first crop. This second crop was harvested after six weeks, when the kernels were at the soft dough stage.

All plant material above the crown was harvested.

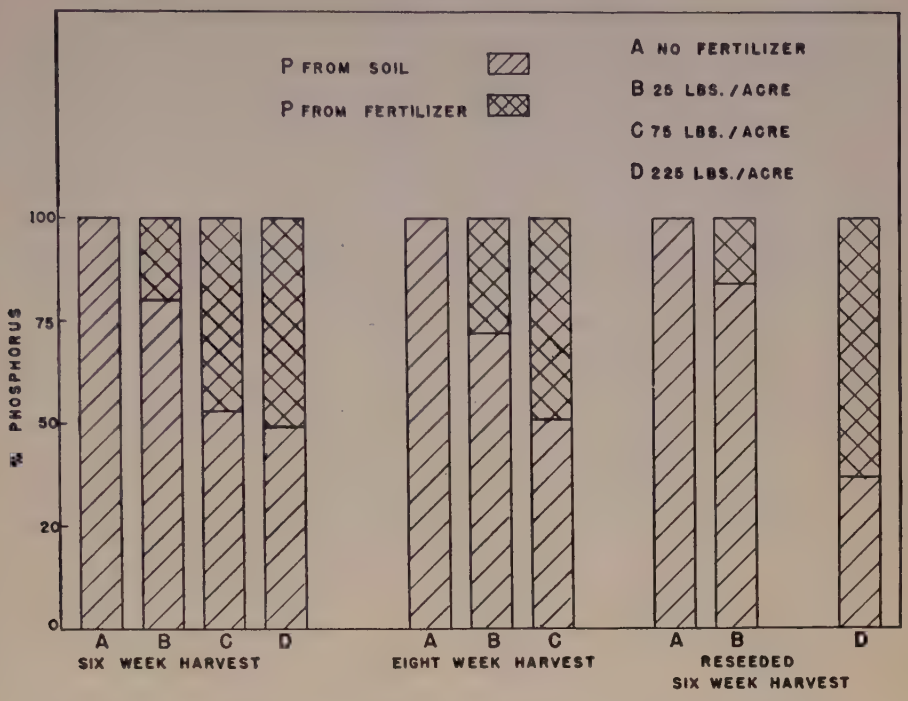

FIGURE 2. Percentage of phosphorus in the plant from soil and fertilizer for different rates of phosphate application.

ANALYTICAL PROCEDURE

The plant material from each pot was wet ashed by the method of Brenner and Harris (4). The resulting solution was made up to 100 ml. and filtered. Aliquots of a suitable size were then taken for both total phosphorus and radiophosphorus determinations. The total phosphorus content was determined colorimetrically using the method of Shelton and Harper (5). The usual procedure for radiophosphorus determination was followed (1). Corrections for self-absorption were used (1).

OBSERVATIONS

The fertilized plants in all cases showed earlier maturity than the checks, a result in accord with field experience.

The data obtained are presented in Table 2, together with the differences between means required to reach the 5 per cent level of significance. The data were analysed statistically according to the methods outlined by Snedecor (6).

A graphical presentation showing the breakdown of total phosphorus into soil phosphorus and fertilizer phosphorus is given in Figures 1 and 2.

DISCUSSION OF RESULTS

Within each harvest date, the amount of phosphorus taken up by the plants increases with increasing rates of phosphorus application, a result similar to those presented by many other workers.

TABLE 2.—SUMMARY OF AVERAGES OF PLANT WEIGHT AND PHOSPHORUS UPTAKE FOR SIX- AND EIGHT-WEEK HARVEST, AND SIX-WEEK HARVEST OF SECOND CROP

	Rate of fert. application, lb./acre	No. of pots	Oven dry wt. plants, gm./pot	Total P, mg./pot	Wt. fert. P used, mg./pot	% of total P from fert.	% of applied P used	Wt. soil P used, mg./pot
6-week harvest	0	6	3.64	11.9	—	—	—	11.9
	25	6	3.76	14.0	2.9	20	15.8	11.1
	75	6	4.39	16.8	7.8	47	14.4	9.0
	225	4	4.57	20.5	10.4	51	6.4	10.1
Least sig. diff. between 225 and any one of the other rates			1.37	2.5	2.1	4	3.4	1.5
L.S.D. between any two of 0, 25 and 75 lb. rates			1.17	2.1	1.8	3	2.9	1.3
8-week harvest	0	6	8.02	14.8	—	—	—	14.8
	25	6	8.51	17.4	4.9	28	27.4	12.4
	75	6	8.35	20.1	9.9	49	18.3	10.1
L.S.D. between means			0.82	0.5	1.3	5	1.9	1.7
Re-seeded 6-week harvest	0	6	1.48	3.1	—	—	—	3.1
	25	6	1.83	3.8	0.6	16	3.5	3.2
	225	4	1.46	4.8	3.0	63	1.9	1.8
L.S.D. between 225 lb. and any one of other rates			0.25	0.6	0.3	4	1.0	0.5
L.S.D. between 0 and 25 lb.			0.21	0.5	—	—	—	0.4

The weight of *fertilizer phosphorus* taken up by the plants similarly increases with increasing rates of phosphorus application. The data show highly significant differences in all cases.

The percentage of total plant phosphorus coming from the fertilizer increases steadily with increasing rates of application, as is to be expected from the data for total phosphorus.

The percentage of applied phosphorus utilized by the plant decreases as the amount of fertilizer applied increases. The value of 27.4 per cent uptake for 25 lb. of ammonium phosphate at the eight-week date is of the same order as other estimates of maximum recovery by more usual methods with other soils and other regions.

The amount of soil phosphorus utilized decreases with increasing rates of applied phosphate in general. For the six-week harvest, the differences are small, but the 75 lb. and 225 lb. rates of application gave results significantly lower than for the unfertilized pots. The eight-week harvest, as would be expected, shows larger differences in uptake of soil phosphorus and these are in all cases significant. These results are in contrast to earlier results reported (1) for a 25 lb. rate of application in a field trial, which showed an increase in the amount of soil phosphorus used as a result of fertilizer application.

The second cropping shows results similar in every way to those of the first cropping, but the actual amounts of phosphorus are smaller in each case. The relatively unsatisfactory growth of these pots (they show less than half the tissue weight of the first crop) is due to the higher, less favourable temperatures prevailing during their growth period. The relatively small amounts of fertilizer phosphorus taken up is probably due partly to the unsatisfactory growing conditions, and partly due to the longer period the fertilizer was subject to fixation reactions in the soils.

Other fertilizers and other methods of application are being tested, and field experiments are planned for the immediate future, to give further information. These results will be published when available.

SUMMARY

Radioactive phosphorus, P^{32}, has been used to measure the uptake of fertilizer phosphorus and soil phosphorus by wheat plants fertilized at the rates of 0, 25, 75 and 225 lb. of $NH_4H_2PO_4$ per acre, and grown in the greenhouse. Under these conditions, the results indicate:

1. With increasing rate of phosphorus application, the amount of fertilizer phosphorus used increases, while the percentage of fertilizer used decreases.

2. The uptake of soil phosphorus is depressed by phosphate fertilizer application, the amount of the depression apparently being a function of the amount of phosphate applied.

ACKNOWLEDGMENTS

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A PRELIMINARY REPORT ON THE USE OF THE LEES AND QUASTEL SOIL PERFUSION TECHNIQUE IN DETERMINING THE NITRIFYING CAPACITY OF FIELD SOILS

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INTRODUCTION

A series of articles by workers at the Unit of Soil Metabolism, British Agricultural Research Council, appeared recently which describes the adaptation of the perfusion technique, a method of proven value in metabolic studies of isolated plant or animal tissues, to similar studies of biological systems in soil (1, 3, 6).

Two of the investigators, Lees and Quastel (3, 4, 5), found this technique to be invaluable in clarifying a number of questions pertaining to the nitrifying processes of soil micro-organisms. A consideration of the latter studies suggests that the soil perfusion technique might prove to be a convenient method of determining the relative nitrifying capacities of different soils, or the influence of different cultural practices on the nitrifying capacity of a given soil. Studies have been undertaken to determine whether such may be the case, and the preliminary results of these investigations are presented in this paper.

EXPERIMENTAL

Apparatus

The perfusion technique, as applied to soil, has been fully described by Lees and Quastel (3). The soil perfusion apparatus used in the present studies was similar to that evolved by Audus (1), with only two changes being introduced. The first was to dispense with the by-pass tube which, as stated by Audus, is not essential to the working of the apparatus. Its omission merely required all air entering the unit to pass through the column of soil, thus ensuring maximum aeration. The second change was the substitution of a cylindrical separatory funnel* for the pear-shaped type used by Audus, and was made because of the difficulty experienced in securing the latter type with a suitable neck.

The apparatus now in use is shown in Figure 1. The glass tube A, 10 × 1 in., contains the soil sample which is held in place between two glass wool plugs. The lower of these is supported by a short length of glass rod B. The separatory funnel C contains the perfusate and has a maximum capacity of 300 ml. The side assembly was constructed by fusing an ordinary test tube D into a length of 4 mm. internal diameter tubing. The unit is connected to a weak vacuum through the short length of thermometer tube E. In operation the vacuum causes air to enter the unit through D. This carries the short column of liquid in the small side tube to the top of the apparatus and as this liquid is discharged on to the soil the vacuum is momentarily released, allowing a fresh supply of liquid to surge up the small side tube, whereupon the cycle is repeated.

* Supplied by The Richards Glass Co., 102 Atlantic Ave., Toronto, Ont.

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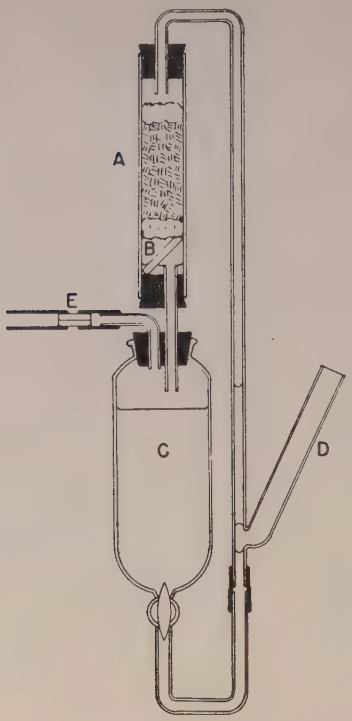

FIGURE 1. Soil perfusion apparatus.

In the present studies a water pump was used to produce the vacuum. Some difficulty was experienced at first because of varying water pressure; however, this has been overcome by placing a control device in the vacuum line.

The taking of samples is a simple procedure, for, with a number of units attached to a vacuum manifold, it is only necessary to release the vacuum when the perfusate in all units will flow into the sampling tubes D from which aliquots for chemical analyses are readily pipetted.

Soil samples were collected in quart jars, spread out in open enamel trays to air dry for 24 to 48 hours, and sieved. Fifty grams of the 1.0 – 3.0 mm. crumb fraction were placed in a unit together with 250 ml. N/50 ammonium sulphate solution, with neither the glassware nor solution being sterilized. The weight of the complete unit was recorded and this, together with a record of the volume of perfusate removed when sampling, made it possible to calculate what the unit should weigh assuming no loss through evaporation. It was a constant practice to weigh the apparatus and adjust for evaporation by the addition of distilled water at least three hours before sampling.

Nitrate Determinations

The rate of nitrification in a perfusion unit was readily ascertained by determining the nitrate-N in the perfusate at intervals of 1 to 7 days, the shorter time interval being used when rates were rapidly changing. The

colorimetric method described by Lees and Quastel (3) was tried but later discontinued in favour of the following modification which in our experience has proven as accurate as the former, while being simpler to perform. In addition it possesses the added advantage of yielding results the same day samples are taken.

An aliquot of the perfusate, or a suitable dilution of the perfusate, such as to contain 10 – 100 micrograms of nitrate-N is placed in a 50 ml. volumetric flask. Add 0.1 ml. of 6 per cent hydrogen peroxide (A.R.) and one drop of a saturated calcium hydroxide solution. Evaporate to dryness in an electric oven at 110° C. Cool and rapidly add one ml. of phenol disulphonic acid reagent. Let stand for ½ hr.; add 10 ml. distilled water and mix. Finally add 35 ml. N/1 sodium hydroxide* and make up to volume. The colour developed is proportional to nitrite plus nitrate-N and may be measured by some type of colorimeter.

In these studies, the colour was read immediately on a Coleman Junior spectrophotometer using a wavelength of 420 mu. with a blank of distilled water carried through the analytical procedure as a reference. Nitrate-N was determined by referring to a calibration curve previously prepared by subjecting standard potassium nitrate solutions to the same procedure.

Although the colour developed is actually proportional to combined nitrite and nitrate-N, since the amount of nitrite-N in the perfusate was found to be relatively low both by Lees and Quastel (3) and in the present experiments, its presence was disregarded and the colour density recorded as nitrate-N. It should be stated, however, that there is now one known substance, namely chlorate ion, which will selectively inhibit the Nitrobacter group thereby causing the accumulation of nitrite rather than nitrate-N (2). The possibility that there may be other substances having the same effect should be kept in mind.

Soil Studies

Our main object in these preliminary studies was to determine whether the perfusion technique would prove sufficiently sensitive, as an indicator of nitrifying capacity of soils, to distinguish differences in the capacity of a soil type subjected to different cultural practices, and whether these differences would be indicated with a reasonable degree of constancy. Most of the samples were obtained from the Horticultural Experiment Station, Vineland Station, Ontario, and, on a soil classified as Vineland Sandy Loam, represented three soil treatments, namely, mulch (in this case legume hay), permanent sod, and a sod which had received several applications of ammonium nitrate. Nitrification curves obtained with replicate samples representing these treatments may be seen in Figure 2. Perhaps the most striking characteristic of these curves, taken as a group, has been the cessation of nitrification when but a relatively small portion of the ammonia-N provided was converted to nitrate-N. The reason for this is believed to be the pH factor, although the possible existence of other causes such as nutritional deficiencies has not been explored. The Vineland Sandy Loam, being extremely low in calcium and magnesium, readily develops strong acidity when treated with acid-forming fertilizers. Thus

* The substitution of sodium hydroxide for the more commonly used ammonium hydroxide was made as a precautionary measure, since ammonia determinations by nesslerization were often run simultaneously.

the fertilized sod, having an initial pH of 4.24, showed no appreciable nitrification even after ten weeks; whereas the sod and the mulched soil samples, starting at pH 6.34 and 6.48, respectively, were capable of nitrifying 80 and 120 p.p.m. of the ammonia-N before the pH fell to 5.0 or below and nitrification ceased.

The Vineland Sandy Loam gave a curve quite different from that reported by Lees and Quastel (3) who used a "rich garden soil." To determine whether this difference resulted from the soil or the methods used, a sample of a rich potting soil was obtained from the Department of Horticulture, Ontario Agricultural College. The nitrification curve of this soil may be seen in Figure 2 and is similar in character to that found by Lees and Quastel.

DISCUSSION

Our preliminary studies into the possible usefulness of the perfusion technique as an indicator of the nitrifying capacity in soils have proven encouraging, in that of the first four soils studied (three of which represent different treatments of a single soil type), four distinct nitrification curves have been obtained. Furthermore the agreement between replicate soil samples, as indicated by the clusters in Figure 2, has been surprisingly consistent. In our opinion one great advantage of the perfusion system over the tumbler or pot method, in which nitrate is measured only at the beginning and end of a 30-day period, is the fact that the nitrate may be determined readily at such a frequency as to outline a complete curve without in any way disturbing the soil. Such a curve yields information concerning three matters of interest: the lag period, the maximum velocity,

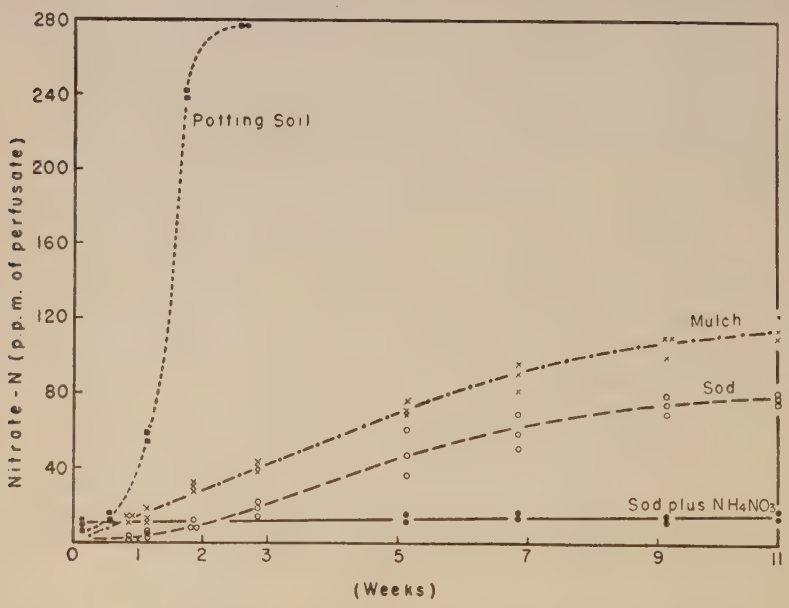

FIGURE 2. Average rates of nitrification obtained with samples of four soils as determined by the soil perfusion technique.

and the amount of ammonia-N the micro-organisms can nitrify in a given soil before some limiting factor brings the process to a halt. The curves for the four soils show differences in all three.

Perhaps the one feature indicated in Figure 2 that provokes the greatest interest is the absence of a lag period with the soil samples collected from beneath the mulch. The perfusion of eight mulched soil samples collected from apple and peach orchards during May, September, October, and January has, without exception, yielded the same result, namely an initial linear relationship between rate of nitrification and time which lasts for a period of three to six weeks before being followed by a period of decreasing nitrification. On the other hand, the soil samples representing sod culture obtained at the same times and locations have invariably shown a lag period of from four to ten days. Since this lag period must be the time required for a reduced population of nitrifying organisms to grow to its environmental limit, the absence of a lag period, as shown by the mulched soil, would apparently indicate that this population is already present at its maximum level. It would appear, excluding a possible differential effect of one or two days' air drying on the number of nitrifying organisms in the two soils, that the application of a legume mulch to Vineland Sandy Loam has maintained, through at least three seasons of the year, the nitrifying organisms in the soil at a maximum level, a condition not found in any of the other soil samples so far studied.

Our investigations into the effect of mulch on the nitrifying capacity of soils are being extended and we hope may be reported in detail later. From the experience gained in these preliminary studies it would appear that the soil perfusion technique should prove a useful addition to the methods presently employed by the microbiologist.

SUMMARY

In preliminary studies using the soil perfusion technique as a means of determining the nitrifying capacity of four soils, four distinct curves have been obtained.

Evidence has been found to suggest that the addition of a mulch of legume hay to Vineland Sandy Loam has stabilized the population of nitrifying organisms at its maximum level.

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